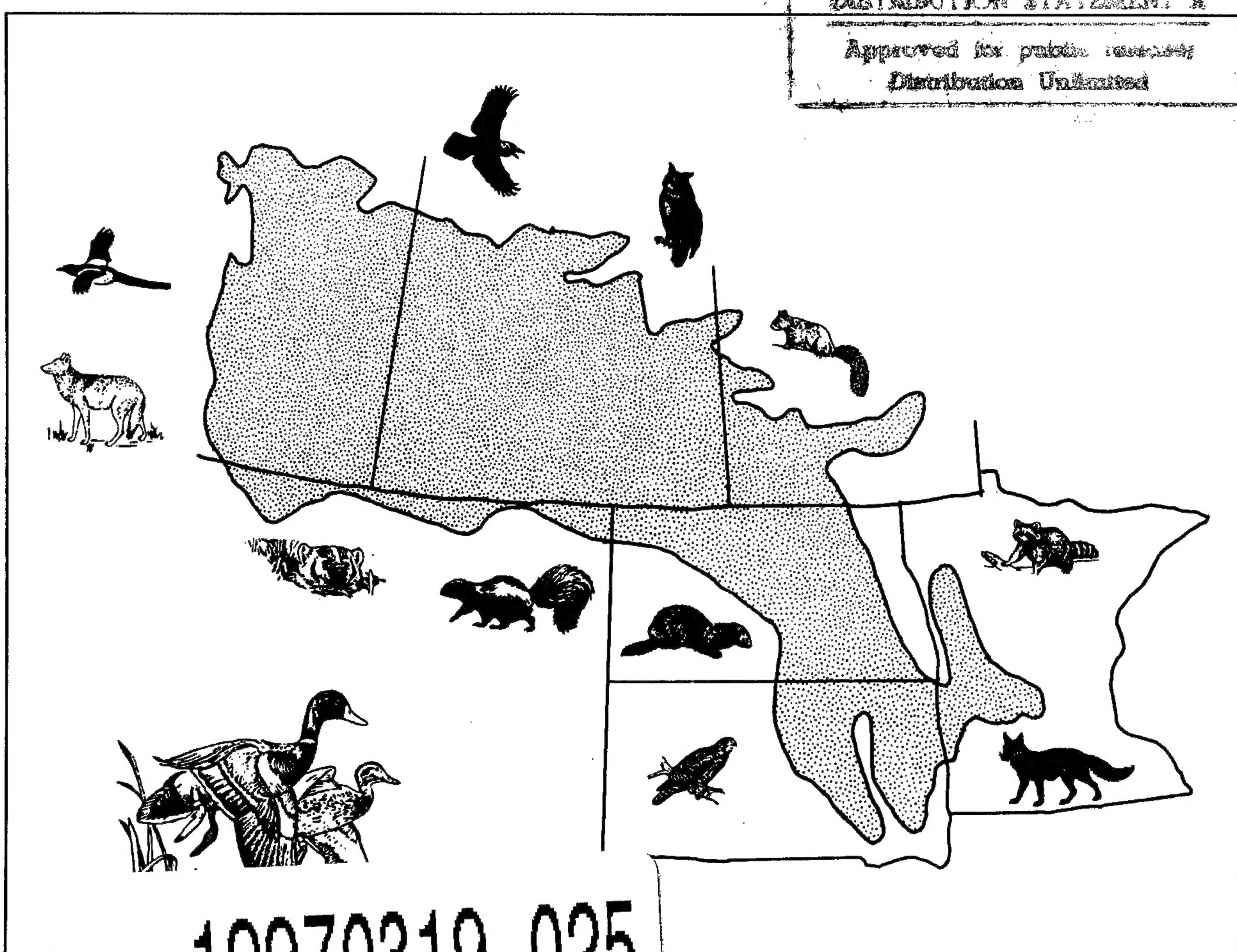
Distribution and Abundance of Predators that Affect Duck Production—Prairie Pothole Region



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Abstract. During 1983–88, the relative abundance of 18 species and species-groups of mammalian and avian predators affecting duck production in the prairie pothole region was determined in 33 widely scattered study areas ranging in size from 23–26 km^2. Accounts of each studied species and species-group include habitat and history, population structure and reported densities, and information on distribution and abundance from the present study. Index values of undetected, scarce, uncommon, common, or numerous were used to rate abundance of nearly all species in each study area. Principal survey methods were livetrapping of striped skunks (*Mephitis mephitis*) and Franklin's ground squirrels (*Spermophilus franklinii*), systematic searches for carnivore tracks in quarter sections (0.65 km^2), daily records of sightings of individual predator species, and systematic searches for occupied nests of tree-nesting avian predators. Abundances of predators in individual areas were studied 1–3 years.

The distribution and abundance of predator species throughout the prairie pothole region have undergone continual change since settlement of the region by Europeans in the late 1800's. Predator populations in areas we studied differed markedly from those of pristine times. The changes occurred from habitat alterations, human-inflicted mortality of predators, and interspecific relations among predator species. Indices from surveys of tracks revealed a decline in the abundance of red foxes (*Vulpes vulpes*) and an albeit less consistent decline in the abundance of raccoons (*Procyon lotor*) with an increase in the abundance of coyotes (*Canis latrans*). Records of locations of occupied nests revealed great horned owls (*Bubo virginianus*) and red-tailed hawks (*Buteo jamaicensis*) tended to nest ≤0.5 km apart, and American crows (*Corvus brachyrhynchos*) tended to avoid nesting ≤0.5 km of nests of red-tailed hawks. Excluding large gulls, for which no measurements of abundance were obtained, the number of predator species averaged 12.2 (SD = 1.60) per study area; common or numerous predator species averaged 6.0 (SD = 1.54) per study area (minimal because the abundance of weasels [*Mustela erminea*; *M. frenata*] in all areas and of minks [*Mustela vison*] and raptors in some areas was not rated). Major changes in relative abundance of individual predator species studied >1 year were few. Predator species most restricted to the aspen parkland were the Franklin's ground squirrel, black-billed magpie (*Pica pica*), American crow (*Corvus brachyrlus*), and red-tailed hawk; species most restricted to the prairie were the badger (*Taxidea taxus*), Swainson's hawk (*Buteo swainsoni*), and ferruginous hawk (*B. regalis*). The coyote, black-billed magpie, and American crow were most numerous in Canada, whereas the red fox, raccoon, mink, ferruginous hawk, and great horned owl were most numerous in the United States. The number of common or numerous egg-eating predator species (excludes large gulls and weasels, which were not rated) averaged 4.6 (SD = 0.90) per

study area. The average numbers of common or numerous egg-eating species per study area did not differ among provinces and states, but birds gradually replaced mammals from southeast to northwest across the region. Investigators are urged to assess composition of predator populations and relative abundance of predator species for evaluations of waterfowl recruitment.

Key words: Avian predators, duck production, history, inter- and intraspecific relations, mammalian predators, predator abundance, predator distribution, population monitoring, population trends, predator communities, prairie pothole region.

The prairie pothole region of North America is vital to the continent's waterfowl. This region of approximately 777,000 km^2 of prairie and aspen parkland habitat presently extends from southeastern South Dakota to central Alberta (Fig. 1) and contains millions of fertile wetlands suited for production of many duck species (Mann 1974; Bellrose 1976). Although the prairie pothole region is only 10% of North America's duck breeding grounds, about half of the continent's ducks fledge there (Smith et al. 1964; Bellrose 1976). Hence, factors of duck production in the region are of special interest to individuals and agencies responsible for the welfare of North American waterfowl populations (Crissey 1969; Pospahala et al. 1974; Bellrose 1976; Turner et al. 1987).

Predation on hens, young, and eggs severely limits duck production in the prairie pothole region (Johnson et al. 1992; Sargeant and Raveling 1992). Most information about predation on duck species

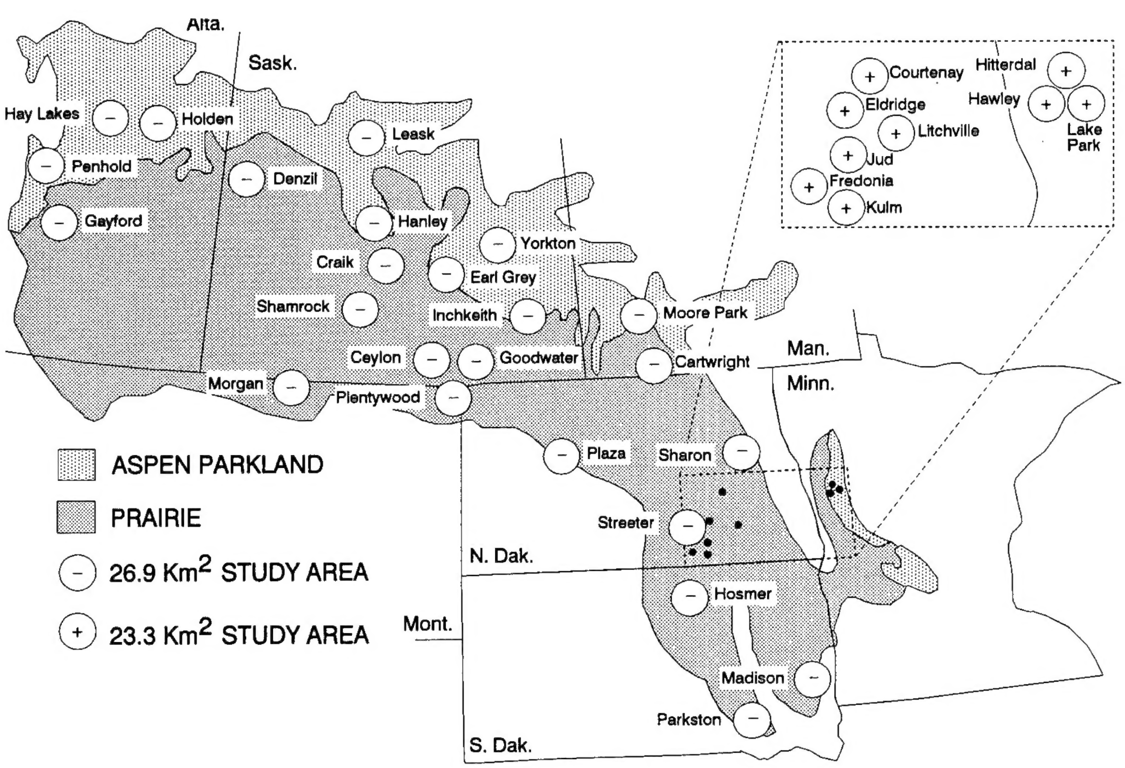


Fig. 1. Prairie pothole region (excludes southwest Minnesota and northcentral Iowa where wetlands are essentially eliminated from extensive drainage [Mann 1974]) with aspen parkland and prairie zones and locations of study areas.

in the region is on the mallard (*Anas platyrhynchos*). Recent studies revealed that mortality rates of mallards during spring and summer averaged 0.19–0.40 for hens, 0.50–0.73 for prefledged young, and 0.88–0.92 for clutches (nests) and that predation was the major cause of mortality (Sargeant and Raveling 1992). Mortality rates of other duck species are also high, and predation is the principal mortality agent (Klett et al. 1988).

Evolutionary adaptations of prairie ducks that minimize the effects of predation include large clutches, renesting, antipredator behaviors, and cryptic coloration of hens. However, the intensity of predation varies with changes in the environment, which can have severe effects on waterfowl populations (Sargeant and Raveling 1992). During the last 120 years, the prairie pothole region has been transformed from largely pristine wilderness to an intensively farmed area (Bird 1961; Kiel et al. 1972; Turner et al. 1987). Coupled with this change have been changes in composition of predator communities and in abundance of nearly all predator species. Presently, most nesting habitat for ducks is fragmented and degraded, and nesting hens and their eggs and ducklings are exposed to different types of predator communities than existed during pristine times (period of recorded history to about 1870; Cowardin et al. 1983, 1985; Greenwood et al. 1987).

Published accounts of predator populations in the prairie pothole region are fragmented and sketchy. In this report, we summarize in species accounts information about the history and population structure of mammalian and avian predator species that affect duck production in the region. We also provide new data on the distribution and abundance of those predator species and discuss factors of predator abundance and the implications of our findings for duck production.

We restricted our evaluations to wild mammals and birds that prey on adult ducks, duck eggs, or ducklings and were resident in one or more study areas. This included nearly all predator species with potential effect on duck production in the prairie pothole region. Among the reptiles and amphibians in the region, only the snapping turtle (*Chelydra serpentina*) has potential to influence duck production. Snapping turtles occur in some permanent wetlands in southern portions of the region (Conant 1958), where they probably take some adult ducks and ducklings (Coulter 1957; Kirby and Cowardin 1986). Certain predatory fishes, especially the northern pike (*Esox lucius*) and largemouth bass (*Micropterus salmoides*), occur in some freshwater lakes, ponds, and rivers of the region where they probably take some ducklings (Lagler 1956). Domestic cats and dogs are abundant throughout the region, but have not been implicated in significant predation on ducks.

The Prairie Pothole Region

Before settlement, the prairie pothole region was largely treeless prairie that merged into transition forest along its eastern, northern, and western edge (Bird 1961; Kiel et al. 1972). This vast expanse was occasionally interrupted by river valleys and groups of forested hills (e.g., Moose Mountains [Saskatchewan], Riding Mountains [Manitoba], Turtle Mountains [Manitoba and North Dakota]). The prairie habitat reflected the region's low to moderate annual precipitation, periodic droughts, uncontrolled prairie fires, and immense herds of bisons (*Bison bison*; Roe 1939; Bird 1961; Lynch 1964; Kiel et al. 1972; Higgins 1986). A zone of trees (primarily quaking aspen [*Populus tremuloides*]) and brush (primarily willows [*Salix* spp.]) around edges of wetlands separated the prairie from the transition forest. This zone, known as the aspen parkland, is included in our definition of the prairie pothole region (Fig. 1). Encroachment of trees and brush into the prairie was held in check by prairie fires, periods of drought, and grazing by ungulates (Archibold and Wilson 1980; Houston and Bechard 1983; Higgins 1986).

Settlement of the prairie pothole region by Europeans began in earnest about 1870 (Strange 1954; Bird 1961; Robinson 1966; Kiel et al. 1972). The building of railroads during the 1880's opened the region to a great influx of settlers who quickly changed the region's economy from hunting and fur trading to farming. Land was surveyed into sections (2.59 km^2) and distributed by the Canadian and United States governments to encourage settlement. Railroad companies and others were granted large blocks of land, much of which they subsequently sold in section and quarter section (0.65 km^2) units. Homesteaders were granted smaller tracts, generally quarter sections (Strange

1954; Robinson 1966; Watkins and Watson 1975). Roads were established on section boundaries (Kiel et al. 1972). Because of this pattern of land ownership and rural development, sections and quarter sections are still clearly discernible in most areas (i.e., marked by roads, trails, fences, and field edges).

Settlement resulted in human exploitation of the region's animal populations and conversion of native grasslands to farmland and pastures (Kiel et al. 1972). Bison herds and uncontrolled fires were largely eliminated by the late 1800's (Kiel et al. 1972; Higgins 1986). Trees and brush invaded portions of the prairie and widened the aspen parkland (Kiel et al. 1972; Edwards 1976; Archibold and Wilson 1980; Houston and Bechard 1983; Higgins 1986). Agricultural development resulted in plowing of most grassland, draining and other modifications of tens of thousands of wetlands, widespread planting of trees for windbreaks, and destruction of woody borders around wetlands (Bird 1961; Robinson 1966; Bellrose 1976; Merriam 1978; Turner et al. 1987). Presently, nearly all land is used to grow crops or graze livestock; in many areas, over 80% of upland is cultivated annually (Higgins 1977; Sugden and Beyersbergen 1984).

a *b* *c* *d*

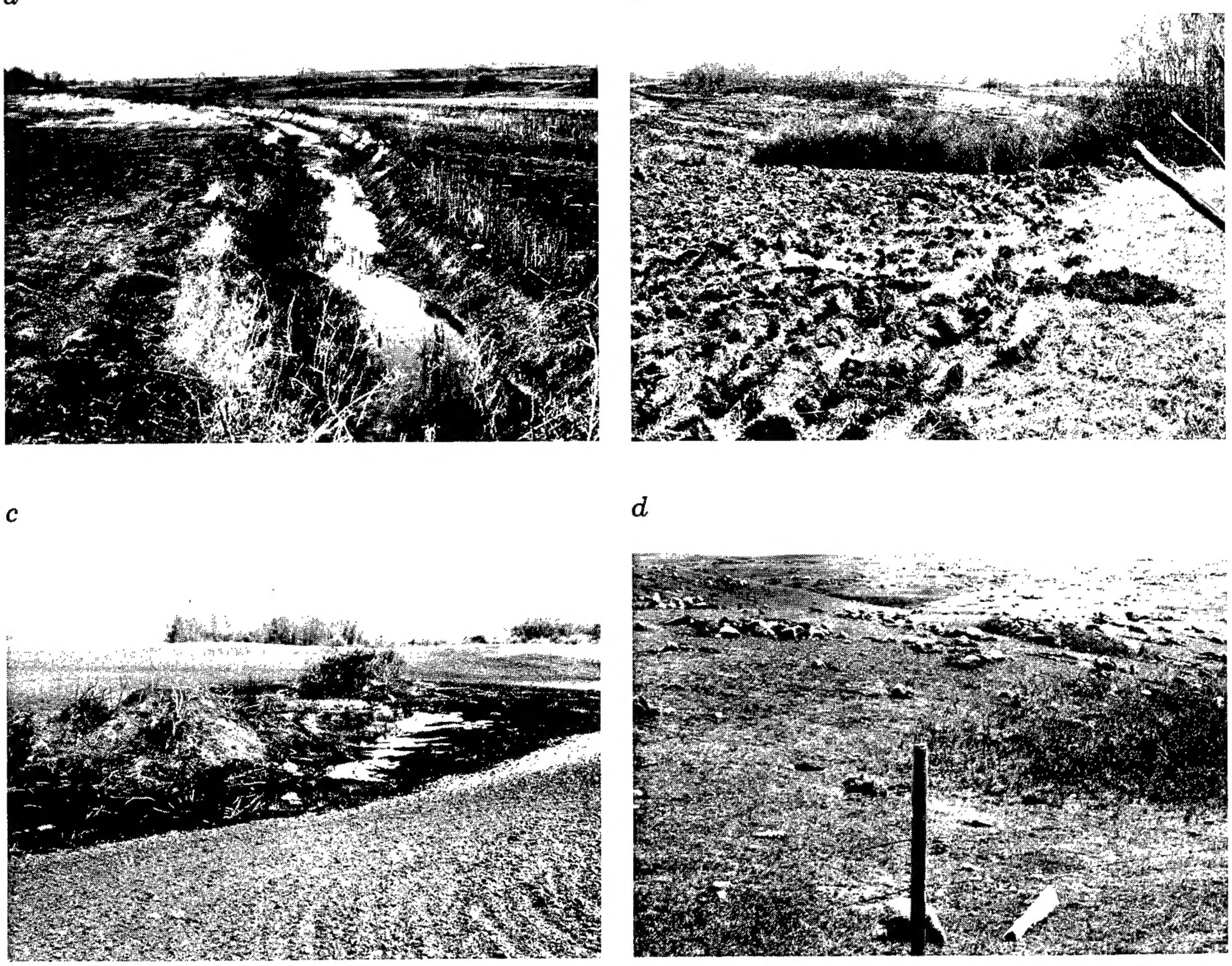


Fig. 2. Habitat modifications in and in the vicinity of study areas in the prairie pothole region during 1983–88: (*a*) drainage of wetlands, (*b*) plowing of native prairie pasture, (*c*) removal of aspen trees around wetland, and (*d*) intensive grazing by livestock and removal of rocks in preparation for plowing.

Anthropogenic habitat changes continue to occur throughout the region (Fig. 2).

Predator populations in the prairie pothole region have been directly affected by humans (e.g., human-inflicted mortality) and by extensive habitat changes from agricultural development. Some predator species that were common and widely distributed before settlement vanished from all or most of the region (e.g., swift fox [*Vulpes velox*], gray wolf [*Canis lupus*]), whereas populations of some other species that were scarce and narrowly distributed expanded greatly (e.g., raccoon [*Procyon lotor*], American crow [*Corvus brachyrhynchos*]; Soper 1946; Adams 1961; Bird 1961; Johnson 1969; Banfield 1974; Cowan 1974; Houston 1977; Jones et al. 1983; Carbyn 1984).

Data Sources

Data on the distribution and abundance of predator species were collected during 1983–88 from 33 study areas throughout the prairie pothole region. The data were collected in conjunction with three studies of duck recruitment: (1) stabilized regulations duck recruitment study (stabilized regulations study) in Alberta, Manitoba, and Saskatchewan (Greenwood et al. 1987); (2) Central Flyway duck recruitment study (Central Flyway study) in Montana, North Dakota, and South Dakota (Johnson et al. 1987); and (3) small unit management study in Minnesota and North Dakota (project document on file at the Northern Prairie Wildlife Research Center).

The stabilized regulations study was conducted during 1982–85, but surveys of predators were not initiated until 1983. Predators were surveyed 1–3 years in 16 study areas: in 4 in Alberta, in 2 in Manitoba, and in 10 in Saskatchewan. The surveys were conducted in 8 areas in 1983, in 10 areas in 1984, and in 10 areas in 1985 (Appendix Table 1).

The Central Flyway study, a companion investigation to the stabilized regulations study, was conducted in nine study areas in the three states during 1983. Predators were surveyed in eight of those study areas: in two in Montana, in three in North Dakota, and in three in South Dakota (Appendix Table 1).

The small unit management study began in 1987 and was conducted in nine study areas: in three in Minnesota and in six in North Dakota (Appendix Table 1). Data from 1987 and 1988 are included in this report. Predators were surveyed in six of the small unit management study areas in 1987 (in two in Minnesota and in four in North Dakota) and in all nine study areas in 1988.

Study Areas

The stabilized regulations and Central Flyway study areas are along aerial survey transects used by the Canadian Wildlife Service and the U.S. Fish and Wildlife Service for estimating annual size of breeding waterfowl populations (Bellrose 1976). These study areas are scattered throughout the prairie pothole region (Fig. 1) and represent principal duck nesting habitats. Each study area is 1.6 × 16 km and most areas include an east–west road or trail (center road) that extends lengthwise through the center (Fig. 3). There is no center road in one study area (Morgan) or in 60% of another (Plentywood). Each study area was divided into 40 legal quarter sections. (The legal descriptions of the centers of the west ends of these study areas are provided in Appendix Table 2, and Fig. 3 shows reference points.)

The small unit management study areas are located three each in three physiographic regions of western Minnesota (Fergus Falls Till Plain) and eastern North Dakota (Drift Plain, Missouri Coteau). They were selected to represent areas with a potential for high duck production but also represent principal habitats of the respective physiographic regions. Each study area contains nine sections arranged in a north–south by east–west cross (Fig. 3). (The legal descriptions of the study area centers are provided in Appendix Table 2; Fig. 3 shows reference points.)

Twenty-one of the 33 study areas are in the prairie and 12 are in the aspen parkland. Topography is relatively level to moderately rolling in all areas (Fig. 4). The climate of the region is subhumid with cold winters and warm summers. In general, snowmelt occurs during late March and April and is delayed with increases in latitude.

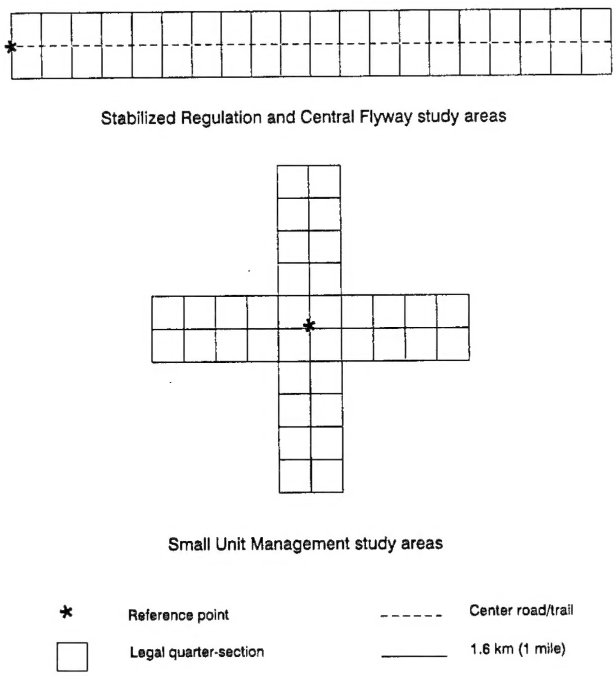


Fig. 3. Configuration of study areas showing the arrangement of quarter section sample units and locations of reference points for legal descriptions (Appendix Table 2).

Most land in each study area is privately owned, but landowners permitted us to work in about 97% of the quarter sections (percentage varied slightly by survey type). Some land in each small unit management study area, including all or part of the center section, is federally owned and managed for waterfowl production (Fig. 4a). Dominant upland habitat types in all study areas are cropland that is cultivated annually and grassland that is grazed by livestock (Table 1). Principal crops are small grains, but include sunflowers in North Dakota and considerable corn and other row crops in Minnesota and South Dakota. Several study areas (Ceylon, Goodwater, Kulm, Shamrock, Yorkton) include portions of large (>10 km^2) pastures (Fig. 4b). Other pastures are also present in most study areas, but nearly all are small units (<3 km^2). Occupied and abandoned farmsteads are scattered throughout each study area. Undisturbed upland habitats consist primarily of wetland edges, small (<2 ha) areas unsuited for agriculture or neglected during farming and grazing, abandoned farmsteads, wildlife management tracts (in some study areas in the United States), and some wooded areas.

Trees are scattered throughout each study area, but are most numerous in study areas in the aspen parkland (Table 1). Most trees in study areas in the prairie are in single-row shelterbelts in fields (Fig. 4c) and in multi-row windbreaks at farmsteads. In the aspen parkland, quaking aspen trees with hazelnut (*Corylus* sp.) or willow understory are prevalent around wetlands and in small woodlots. Oak trees (*Quercus* spp.) are common in woodlots in the three study areas in Minnesota. Woodlots of up to 0.65 km^2 are present in six study areas (Hay Lakes, Hawley, Hitterdal, Holden, Leask, Yorkton). Additional data on physiography, habitats, and land-use in the prairie pothole region are provided by Bird (1961), Coupland (1961), Kiel et al. (1972), Stewart and Kantrud (1972), Brewster et al. (1976), and Cowardin et al. (1985).

Mammalian predators were removed annually from April through June on federal land in the center of three small unit management study areas (Eldridge, Fredonia, Lake Park). The removal was part of an evaluation of effects of localized removal of predators on nest success in ducks. No other known organized removal of predators with probable influence on our findings occurred. However, furbearers were trapped in all study areas, and in five study areas (Ceylon, Hanley, Litchville, Shamrock, Penhold), we found evidence of indiscriminate killing of predators.

Predator Species

Fifteen predator species and groups of related predator species were selected for assessment. These included seven carnivore species and species-groups (coyote [*Canis latrans*], red fox [*Vulpes vulpes*], raccoon, striped skunk [*Mephitis mephitis*], badger [*Taxidea taxus*], mink [*Mustela vison*], and two weasels [*M. erminea* and *M. frenata*]); one rodent (Franklin's ground squirrel [*Spermophilus franklinii*]); two corvids (American crow and black-billed magpie [*Pica pica*]); and five raptors (northern harrier [*Circus cyaneus*], Swainson's hawk [*Buteo swainsoni*], red-tailed hawk [*B. jamaicensis*], ferruginous hawk [*B. regalis*], and great

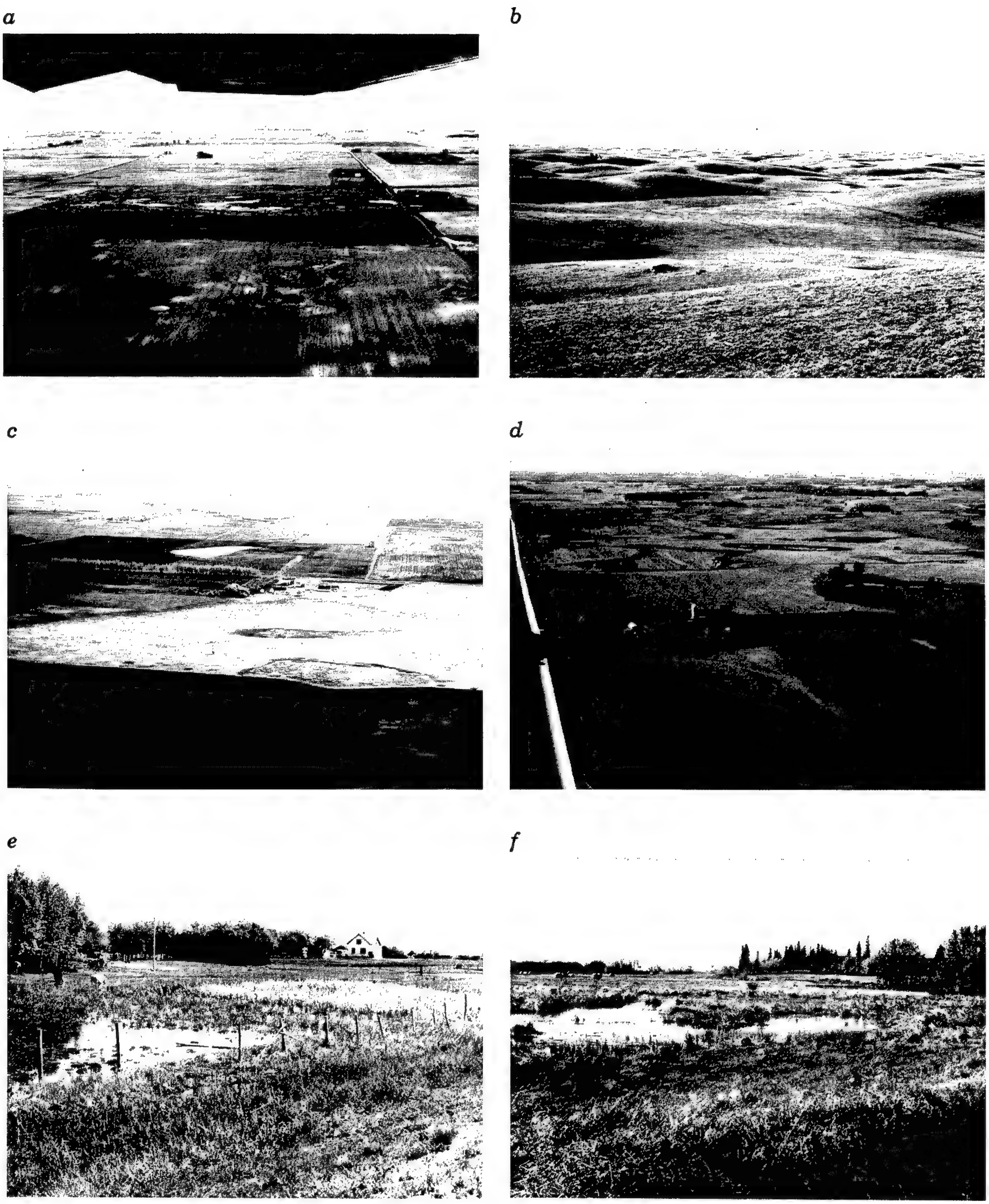


Fig. 4. Examples of aspen parkland and prairie habitats that comprised the study areas in the prairie pothole region where predator surveys were conducted during 1983–88: (*a*) aerial view of the Eldridge study area showing central quarter section of federal Waterfowl Production Area, (*b*) large grassland pasture in the Shamrock study area, (*c*) shelterbelts near the Courtenay study area, (*d*) aerial view of the Lake Park study area, (*e*) roadside habitat in the Yorkton study area, and (*f*) aspen parkland–forest habitat in the Leask study area.

Table 1. *Habitat composition (%) of study areas in the prairie pothole region where predator populations were assessed during 1 or more years, 1983–88.*

Area[b]	Habitat types[a]					
	Cropland	Grassland[c]	Woodland	Wetland	Odd area[d]	Barren[e]
Canada						
Alberta						
Gayford	30	50	1	14	4	1
Hay Lakes*	44	23	10	16	5	1
Holden*	45	24	7	17	5	1
Penhold*	50	21	5	19	5	1
Manitoba						
Cartwright	66	19	2	7	6	1
Moore Park*	62	8	6	14	9	1
Saskatchewan						
Ceylon	56	31	tr[f]	9	3	1
Craik	84	3	1	7	5	1
Denzil	76	9	1	7	6	1
Earl Grey*	80	2	4	8	6	1
Goodwater	50	36	tr	9	4	1
Hanley*	70	11	2	11	5	1
Inchkeith*	71	10	4	5	8	1
Leask*	40	26	16	12	5	1
Shamrock	59	29	tr	7	4	1
Yorkton*	45	25	14	11	5	tr
United States						
Minnesota						
Hawley*	45	24	12	14	5	tr
Hitterdal*	61	12	6	17	4	tr
Lake Park*	57	17	5	17	4	tr
Montana						
Morgan	17	79	0	4	tr	tr
Plentywood	45	37	tr	16	2	tr
North Dakota						
Courtenay	71	11	1	12	5	tr
Eldridge	81	6	2	9	2	tr
Fredonia	12	37	tr	46	5	tr
Jud	58	21	1	14	6	tr
Kulm	33	43	1	19	4	tr
Litchville	54	20	2	20	4	tr
Plaza	55	27	tr	15	3	tr
Sharon	79	7	tr	10	4	tr
Streeter	40	38	tr	14	8	tr
South Dakota						
Hosmer	36	49	tr	10	5	tr
Madison	72	16	tr	5	7	tr
Parkston	47	40	1	7	5	tr

[a] Habitat determinizations were by the U.S. Fish and Wildlife Service National Wetland Inventory from interpretations of aerial photographs of May and July 1982 (all study areas in Canada, Montana, South Dakota, and the Plaza, Sharon, and Streeter study areas in North Dakota) and from outdated photography that was ground-truth corrected in 1987 (all areas in Minnesota and in the Courtenay, Eldridge, Fredonia, Jud, Kulm, and Litchville study areas in North Dakota). See Cowardin et al. (1985) and Greenwood et al. (1987) for details of habitat classification.

[b] Study areas denoted with an asterisk (*) are in the aspen parkland, all others are in the prairie.

[c] Includes hayland.

[d] Includes many different small features such as farmsteads and gravel pits (Cowardin et al. 1985).

[e] Barren habitats are roads and similar non-farmed areas.

[f] tr = <0.50%.

horned owl [*Bubo virginianus*]). Incidental data were also collected on the gray wolf, common raven (*Corvus corax*), ring-billed gull (*Larus delawarensis*), and California gull (*L. californicus*).

All carnivores in our surveys are known predators of adult ducks, duck eggs, or ducklings (Keith 1961; Teer 1964; Balser et al. 1968; Dzubin and Gollop 1972; Duebbert and Lokemoen 1976; Talent et al. 1983; Sargeant and Arnold 1984; Sargeant et al. 1984; Arnold and Fritzell 1987b; Fleskes 1988). Although three species of weasels are common in the region, we included only the ermine and long-tailed weasel in our surveys and did not distinguish between them. The third species, least weasel (*Mustela nivalis*), weighs less than 65 g and eats mice, voles, and other small prey (Banfield 1974; Jones et al. 1983). Whereas predation on waterfowl by the raccoon, striped skunk, and badger is almost exclusively on eggs, the other species also prey on adults and ducklings (Sargeant and Arnold 1984). We included the gray wolf in our species accounts because of its importance to understanding changes in canid populations in the region and because evidence of a resident gray wolf was found in one study area. Also, gray wolves prey on waterfowl and waterfowl eggs (Timm et al. 1975; Raveling and Lumsden 1977). The only other wild mammalian carnivores detected in our surveys were the black bear (*Ursus americanus*) and the river otter (*Lutra canadensis*). We excluded these from our species accounts because we had no evidence of resident individuals in any study area. A black bear was seen once in one study area (Lake Park) and tracks of a black bear were found once in 1 quarter section of another study area (Hawley), where also tracks of a river otter were found once.

The Franklin's ground squirrel is the only rodent believed to affect duck production in the prairie pothole region (Sowls 1948; Sargeant and Arnold 1984; Greenwood 1986; Sargeant et al. 1987b). Franklin's ground squirrels prey on duck eggs (Sargeant et al. 1987b) and occasionally kill ducklings (Sowls 1948).

The two species of corvids in our predator surveys (black-billed magpie and American crow) prey on waterfowl eggs (Kalmbach 1937; Williams and Marshall 1938; Sowls 1955; Anderson 1965; Jarvis and Harris 1971; Dzubin and Gollop 1972; Jones and Hungerford 1972). Both species also prey occasionally on ducklings (Linsdale 1937; Sowls 1955; Sutherland 1982). We included the common raven in our species accounts because it was regularly seen in one study area and preys on waterfowl eggs and young (Jarvis and Harris 1971). No other corvids are known to affect duck production in the prairie pothole region.

The five raptors treated in our species accounts are all relatively large, widely distributed, and at least locally common (Bent 1961; Robbins et al. 1983). Their diets consist primarily of small mammals and small birds, but include some ducks (McAtee 1935; Errington et al. 1940; Todd 1947; Hecht 1951; Houston 1960; Bent 1961; Luttich et al. 1970; McInvaille and Keith 1974; Dunkle 1977; Sherrod 1978; Blohm et al. 1980; Schmutz et al. 1980; Gilmer et al. 1983; Gilmer and Stewart 1983, 1984; Brace 1988). Raptors seldom prey on duck eggs, although northern harriers occasionally take unhatched and pipping eggs (Balser et al. 1968; Willms and Kreil 1984). Other raptors that could affect waterfowl production were either scarce in the few areas where they occurred (e.g., bald eagle [*Haliaeetus leucocephalus*], osprey [*Pandion haliaetus*], prairie falcon [*Falco mexicanus*], peregrine falcon [*F. peregrinus*]) or are migrants that seldom nest in the region (e.g., rough-legged hawk [*Buteo lagopus*]). The only other mid-size or larger raptor species known to be resident in any study areas were the Cooper's hawk (*Accipiter cooperii*), for which a single nest was found in one study area (Lake Park); broad-winged hawk (*B. platypterus*), for which a single nest was found in another study area (Yorkton); and long-eared owl (*Asio otus*) and short-eared owl (*A. flammeus*), both of which nested in several study areas.

We included two of three species of gulls that are common breeding residents in the prairie pothole region in our list of treated species even though we conducted no systematic surveys of the abundance of gulls. The large ring-billed gull and slightly larger California gull were included because both species, especially the California gull, occasionally prey on duck eggs and ducklings (Greenhalgh 1952; Odin 1957; Anderson 1965; Vermeer 1970; Duncan 1986) and incidental data revealed they were common or numerous in several study areas. The small Franklin's gull (*Larus pipixcan*) was excluded because it has not been implicated in predation on duck eggs or ducklings. Other species

of gulls are occasionally seen in the region, but rarely nest there (Salt and Salt 1976; South Dakota Ornithologists' Union 1991).

Predator Surveys

Predator surveys were conducted to determine the distribution and relative abundance of each predator species in each study area. Surveys had to be simple and easily integrated with other study objectives, namely obtaining data on nest success in ducks. For most predator species, proven methodology for assessing abundance was unavailable or cost prohibitive (Clark and Andrews 1982; Greenwood et al. 1985). Therefore, we devised a variety of survey methods that could be systematically applied during the duck nesting season, allowing us to capitalize on observations by the numerous individuals already working in each study area. Spring is a good time to survey predator populations because most predators are caring for young. As a result, surveys can be conducted when populations are relatively stable (little emigration or immigration) and comprised of relatively evenly spaced social groups. More than one survey method was used for some species (Appendix Table 1). (Results from all surveys by study area and year are provided in the Appendix to enable others to combine or use data differently.)

Predators were surveyed by persons or crews whose primary duty was to gather data on nest success in ducks, by other biologists working in the study areas, and by specialists in surveys of predators who moved among study areas. Each crew was responsible for gathering data in two or three study areas in a given year. Individuals responsible for conducting surveys and for maintaining records were instructed in survey methods and given written survey guidelines.

The surveys of predators consisted of (1) livetrapping striped skunks, (2) livetrapping Franklin's ground squirrels, (3) counting carnivore tracks, (4) recording sightings of predators, (5) counting American crows and black-billed magpies along road transects, and (6) recording locations of occupied nests of avian predators. However, not all surveys were conducted each year or in all study areas (Appendix Table 1). In addition to conducting the described surveys, field personnel were asked to record locations of active coyote and red fox rearing dens (dens with pups) and to record information about predator species not accommodated in the systematic surveys. Sources of supplementary data were aerial searches for coyote and red fox rearing dens (Sargeant et al. 1975) in about half of each small unit management study area and records of predators removed from federal lands in central portions of three small unit management study areas.

All surveys except counts of American crows and black-billed magpies along road transects in two study areas (Morgan, Plentywood) and records of predator sightings were conducted inside study areas. The road-transect counts of American crows and black-billed magpies for two study areas (Morgan, Plentywood) were conducted primarily along roads adjacent to each area because of absence of a center road. Data on predator sightings in the small unit management study areas and in some other study areas included time spent in lands adjacent (<2.4 km) to those areas, where some study personnel were also required to work. All data from surveys of predators except sightings were recorded by quarter section or combinations of quarter sections.

The removal of predators from three study areas (Eldridge, Fredonia, Lake Park) was part of the small unit management study. The removal was conducted annually from early April through late June in a 63–303 ha tract of federal land in the center of each area (Appendix Table 3).

Livetrapping Striped Skunks

This survey was conducted in early May and consisted of setting one single-door, wire-mesh livetrap (23 × 23 × 66 cm) for 5 days in each quarter section along the center road for a maximum of 200 trap-nights (one trap set for 1 night) per study area. Traps were moved each day; trap sites in the same quarter section were >100 m apart. Trapping in each study area was conducted on consecutive days. If it was interrupted by inclement weather, it was resumed when conditions improved. Traps were baited with canned sardines and set in the most suitable sites (e.g., field edge, culvert, marsh edge, road ditch), usually <50 m

from the center road. Because striped skunks are largely nocturnal (Jones et al. 1983), traps were set daily between 1700 h and sunset and checked the next morning between sunrise and 0900 h. Caught animals were released at capture sites when traps were checked. The index from this survey was capture rate (the sum of caught skunks divided by the sum of trap-nights).

Livetrapping Franklin's Ground Squirrels

This survey was conducted in early July and consisted of setting four livetraps (same trap described for striped skunks) for 5 days in a cluster along each linear 1.6 km of the center road of each study area for a maximum of 200 trap-days (one trap set for 1 day) per study area. Traps were moved each day to a new site; traps in a cluster were >20 m apart and trap sites were >200 m apart. A trap site was defined as an area ≤2 ha. Trapping was conducted on consecutive days. If it was interrupted by inclement weather, it was resumed when conditions improved. Traps were baited with canned sardines and set in the most suitable sites (e.g., brush or densest available upland vegetation) <400 m from the center road. Traps were set daily between sunrise and 0900 h, left overnight, and checked the next morning during the same time period. We assumed all captures occurred during daytime because Franklin's ground squirrels are diurnal (Choromanski-Norris et al. 1989). Caught animals were released at capture sites when traps were checked. The most useful index from this survey was capture rate (the sum of caught Franklin's ground squirrels divided by the sum of trap-days). The percentage of 2.6-km^2 units of each study area in which Franklin's ground squirrels were caught was useful for describing distribution in study areas.

Counting Carnivore Tracks

The survey of carnivore tracks was a modification of the survey of scent stations designed to index coyote abundance (Linhart and Knowlton 1975; Roughton and Sweeny 1982). Rather than using scent tabs to attract predators to small prepared sites where their tracks could be detected, we relied on personnel experienced in identification of tracks to find tracks at available unprepared sites in quarter-section search units. This modification was made possible by the abundance of good tracking media (exposed soft soil) at many sites (e.g., muddy wetland edges, gravel road edges, dirt trails, field edges) in nearly all quarter-sections during at least one search period. Our premise was that if a carnivore species regularly visited a quarter section, its presence was soon revealed by observable tracks at one or more locations, provided sites and conditions were suitable for finding tracks.

The survey consisted of searching for tracks of the coyote, red fox, raccoon, striped skunk, badger, and mink during two periods (April–mid-May, late May–late June) in each quarter section of each study area (only a mid-May–late June search was conducted in the Central Flyway study areas because of staff shortages). The decision to conduct two searches during these periods was based on examination of data from Canada in 1983 when four searches were conducted. Observers were instructed to wait at least 2 days after precipitation that destroyed tracks before conducting searches and to spend ≤0.5 h in each quarter section examining the most suitable sites for tracks of each species. All-terrain vehicles were used where permitted by landowners to facilitate rapid coverage of study areas. Two observer-days (one observer for 1 day) were required to search each study area once.

Results of track surveys were expressed as the percentage of searched quarter sections in which tracks of each species were found at least once during both searches combined. Data from the Central Flyway study areas, which were searched once, were expanded to estimate results as if they had been searched twice. We used data from study areas that had been searched twice to arrive at regression equations relating percentage of searched quarter sections by study area in which tracks of that species were found in either search to the percentage of searched quarter sections in which tracks were found during only the late search. We applied the regression equations to study areas that had been searched only once to estimate results as if the areas had been searched twice. The correlations between results from the double-search and single-search surveys for individual species ranged from

$r = 0.75$ to $r = 0.93$. The statistical procedures for the expansions resulted in assigning limited occurrence of a species to a study area even if no tracks of that species were found. However, we classified as undetected each species for which no tracks were found, unless we had evidence substantiating its presence (e.g., sighting).

The survey of tracks differentiated better among low than high populations because presence of a single individual was likely to be detected in more than 1 quarter section. When a species became sufficiently abundant to regularly leave tracks in nearly all quarter sections, higher abundance could not be detected.

Recording Sightings of Predators

The number of places in which a predator species was seen daily was recorded. (A place was defined as a 150-m diameter area, about equal to an average size farmstead). This, rather than the number of observed individuals, was selected as the abundance indicator to minimize influence of sightings of groups (e.g., flocks, litters at dens). Each day, each person working in a study area for >0.5 h independently recorded this information and the number of hours spent in the area. Moving predators were recorded only where first seen, and repetitive daily sightings of the same species in the same place were recorded only once by that person for that day.

We anticipated observers would have difficulty remembering exact numbers of places where they saw conspicuous common predator species (black-billed magpie, American crow, large hawks). We initially established, therefore, five categories for numbers of daily sightings of each species and species-group (none, 1–5, 6–10, 11–20, >20). In using observations recorded in this manner, we assigned each daily entry the midpoint value of the indicated category; the value of 21 was assigned to entries in the >20 category. The resulting data were inadequate to differentiate abundance among study areas where populations were low (most study areas). During the small unit management study, we requested that observers record daily the actual number of places where they saw predators. Large hawks were combined into a single category because of the difficulty of identifying hawks. However, observers competent in hawk identifications were instructed to list daily the relative abundance or number of individuals of each observed species.

Results for all observer-days were combined to calculate the average number of places where predators were seen per hour (observation rate). This index was especially useful for describing relative abundance of secretive species likely to be seen often when abundant (e.g., Franklin's ground squirrel, mink, weasels). The index was not useful for describing relative abundance of species unlikely to be seen, even when relatively numerous (most mammalian carnivores), or of low-density species likely to be seen repeatedly at conspicuous locations (e.g., great horned owls at nests and red foxes at dens near roads). For all species, however, the recorded sightings helped document species presence in study areas.

Counting American Crows and Black-billed Magpies Along Road Transects

For this survey, an investigator drove the 16-km center-road of each study area or nearby road if no center-road was available. The investigator stopped at the midpoint of each quarter section and for 1 min counted all American crows and black-billed magpies seen within 0.20 km (survey plot) of the vehicle in each of the 2 adjacent quarter sections (one on each side of road). The investigator also recorded presence or absence of each species in each quarter section as detected by sight or sound while at each stop and while driving between stops. Birds observed departing a survey plot or quarter section were counted only at the site where first seen. The survey period was 2 h after sunrise to 2 h before sunset, but most counts were made during 1000–1500 h. Counts were not conducted during inclement weather or when winds exceeded 28 km/h. The sampling scheme for study areas in Canada consisted of three counts (on different days) made during each of four sample periods (early May–mid-May, late May–early June, mid-June–late June, and early July) for a total of 12 counts for each study area. Nine counts during the first three sample periods were scheduled for the Central Flyway study areas in the United States.

The numbers of counts in individual study areas varied somewhat (Appendix Table 4).

For our purposes, the most useful index from this survey was average percentage of quarter sections in which each species was detected (seen or heard) because distribution and abundance of breeding pairs were better reflected by this parameter than by numbers of detected individuals. The average number of detected American crows and black-billed magpies was unduly influenced by sightings of grouped birds (110 American crows in one instance) that presumably included many transitory individuals. Data from all counts for a study area were averaged because analyses revealed no differences in counts among survey periods.

Recording Locations of Occupied Avian Predator Nests

One of the most reliable methods for estimating numbers of breeding avian predator species is intensive searches for nests (Fuller and Mosher 1981). Study personnel recorded locations of occupied nests of American crows, great horned owls, and large hawks (northern harrier or larger) in each study area. Occupied nests contained eggs or young or were tended by adults (Postupalsky 1974). After 1983, this survey was expanded to include a systematic search for occupied nests of these avian predators (except northern harrier) of all wooded habitat in each study area during late May–early June. The search for nests of great horned owls was advanced to early April in 1987 in the small unit management study areas. This resulted in two complete searches of all wooded habitat in those study areas, one for nests of great horned owls and one for nests of other large raptors.

With these procedures we located nearly all occupied nests of American crows and large hawks, except northern harriers. We had little difficulty finding and determining occupancy of the large, open, deep-cupped nests of American crows (Bent 1964) and the bulky, stick-layered nesting platforms used by raptors (Bent 1961). Eggs and young of American crows could often be seen by looking into nests from above (we used mirrors on extendable poles to examine many nests). Incubating females of all species were often seen from the ground, and adults were usually seen defending nests, especially after eggs had hatched. Nests of northern harriers are usually inconspicuous in dense cover on the ground and in wetlands (Sealy 1967; Duebbert and Lokemoen 1977; Evans 1982; Bildstein and Gollop 1988). Thus, we conducted no systematic searches for nests of northern harriers. Instead, reported nests of northern harriers were found opportunistically, primarily during searches for duck nests (see Greenwood et al. 1987 and Johnson et al. 1987 for details about searches for duck nests). Ferruginous hawks also occasionally nest on the ground (Lokemoen and Duebbert 1976; Gilmer and Stewart 1983; Schmutz 1984), but such nests are conspicuous and usually on hills in open grassland areas (Stewart 1975; Gilmer and Stewart 1983).

Great horned owls usually nest in old nests of other species such as red-tailed hawks (Orians and Kuhlman 1956; Dunstan and Harrell 1973; Houston 1975; Petersen 1979; Bohm 1980), we had little difficulty finding the adopted nests because they offer little concealment to adults and young. However, nesting begins in late February (Stewart 1975) and some young have departed nests by early June (Bent 1961). Our systematic searches were conducted in 1985 and 1986.

We conducted no systematic searches for occupied nests of black-billed magpies. Although the large, woven-domed stick-nests of black-billed magpies (Bent 1964) were easy to find, the species sometimes builds false nests (Linsdale 1937) that may last for years. Moreover, whether a nest is occupied is often difficult to determine because eggs and young are deep inside and not easily observed and adults tending nests are secretive. We recorded locations of occupied nests that we found opportunistically.

We could seldom account for nests that failed before surveys began. Also, searches did not account for unmated and paired adults that did not nest. The proportions of birds without nests of some species, especially the great horned owl, in local populations probably varied and could have been substantial (Adamcik et al. 1978; Houston 1987).

Treatment of Data

All data were examined and records of unusual occurrences (e.g., sighting of locally rare species)

were excluded unless discussion with the observer(s) convinced us of their authenticity. All calculations of species abundance are based on portions of study areas that were actually searched. We averaged annual results for study areas with >1 year of data to obtain single index values of abundance for each species and species-group. Averaging of annual results was necessary to avoid the problem of nonindependence of repeated observations in the same study area. Correlation and other statistical analyses were performed on averages of the annual values of >1 year of data per study area and on the single annual value of 1 year of data per study area. The term "study area- year" is used to refer to data gathered in one study area during 1 year. Two-sample *t*-tests were used to compare means (Snedecor and Cochran 1980) between data sets from various geographic areas. Before performing such tests, we verified equal variances (Snedecor and Cochran 1980). Chi-squared tests of homogeneity were used to compare percentages between data sets from various geographic areas (Snedecor and Cochran 1980). Differences were declared significant if $P \leq 0.05$. We provide standard deviations (SD) for means, but not for percentages (Θ) where sample sizes (*N*) are provided and readers can calculate values (i.e., SD = $\sqrt{(\Theta \div 100) \times (1\ \mathrm{M} - ([\Theta \div 100]) \div N}$.

To assign abundance, we established a range of index values for each species and species-group from our data and from published information and adjusted the index to a scale of 0–100. The abundance scale was partitioned as follows: 0 = undetected, 1–5 = scarce, 6–25 = uncommon, 26–75 = common, 76–100 = numerous. All ratings of undetected were elevated to scarce or uncommon if other evidence revealed presence of the species. The rating of scarce was for species detected only once or twice and at only one or two locations. The albeit subjectively established abundance categories provided criteria for quantitatively describing species abundance in familiar terms.

Partitioning of data sets for comparisons was primarily by habitat zone (prairie versus aspen parkland), country, state or province, and combinations of these. This partitioning reflects major habitat subdivisions and provides tailored data summaries for government agencies responsible for management of waterfowl and predators in the prairie pothole region.

We investigated possible effects on abundance of certain carnivores and on spacing of nests by some avian predator species (certain raptors, American crow) from interspecific relations. For selected pairs of carnivore species, we used correlation analysis (Snedecor and Cochran 1980) to examine the relation between percentage of quarter sections of each study area with tracks of one predator species and percentage of quarter sections of each study area with tracks of the other species. Negative correlations were interpreted as indicating avoidance of one species by the other and positive correlations as indicating interspecific tolerance or attraction of at least one species by the other. In each study area, we examined the relation between the proportions expected by chance and observed proportions of occupied nests of selected pairs of avian predator species that were near (≤0.5 km) each other. We assumed that adult birds tending nests within 0.5 km of each other had overlapping home ranges and high potential to interact, and that if two species avoided nesting near each other, at least one of the species tended to exclude the other. Conversely, two species nesting near each other inferred at least one of the species benefitted or that local habitat features facilitated nesting in close proximity.

We used SAS software (SAS Institute Inc. 1988) to simulate expected distributions of minimum distances between occupied nests for each combination of pairs of avian predator species. We examined whether nest locations of the species most likely to be repelled or attracted (affected species) were independent of those of the other species (effector species). Most raptors are portrayed as interspecifically aggressive (McInvaille and Keith 1974; Schmutz et al. 1980; Rothfels and Lein 1983), but no clear dominance hierarchy has been established among species we tested. Therefore, we labeled the later nesting species of each pair as the affected species. For tests of raptors and American crows, we labeled the American crow the affected species, even though American crows have been known to depredate clutches of Swainson's hawks (Dunkle 1977). For each pair of species, we compared the expected with the observed number of occupied nests of affected species that were ≤0.5 km of occupied nests of effector species. Our rationale was that, if affected species avoid nesting near the effector species, fewer than the number of expected nests are within 0.5 km of each other.

Similarly, if more than the expected number of nests are within 0.5 km, the affected species is selectively nesting near the effector species.

The simulations resulted in two-by-two contingency tables for each species pair in each study area with nests of both species. The results in each study area were combined to assess the tendency of the affected species to avoid or be attracted by the effector species. We used the Mantel and Haenzel method (Fleiss 1973), which also provided a test for how consistent the tendency was by pairs among study areas. In addition, the odds ratio (Fleiss 1973) compared the expected and observed chance of a nest being within 0.5 km of a nest of the other species. Odds ratios significantly >1.0 provided evidence that the affected species selectively avoided nesting near the effector species, and ratios significantly <1.0, that the affected species selectively nested near the effector species.

We also examined intraspecific spacing of nests of certain raptors and the American crow. To do this, we compared the expected with the observed number of nests of a given species within 0.5 km of a conspecific's nest and assumed that all breeding pairs positioned nests independently of one another. Simulations were again used to generate the expected distributions of minimum distances.

Rationale, Data Types, and Criteria to Rate Species Abundance

Carnivores

In general, adults of all carnivore species we studied, except weasels and female minks, have large home ranges (usually several square kilometers or larger), travel extensively (usually several kilometers or more daily), and use a variety of habitats (Sargeant 1972; Sargeant and Warner 1972; Ewer 1973; Fritzell 1978a, 1978b; Andelt and Gipson 1979; Lampe and Sovada 1981; Greenwood et al. 1985; Arnold and Fritzell 1987a; Novak et al. 1987; Sargeant et al. 1987a). Thus, tracks can be a sensitive indicator of the presence and relative abundance of a carnivore species.

We used the percentage of searched quarter sections in which tracks were found to rate abundance of all carnivore species, except weasels. Ermines and long-tailed weasels are small and lightweight (Banfield 1974) and, therefore, reliable searches for their tracks could not be conducted. The only obtained data on weasels were observation rates, which were insufficient to rate abundance in individual study-areas. Data from track surveys were supplemented with locations of active rearing dens (coyote, red fox), systematic livetrapping (striped skunk), and sightings of individuals (mink). Data on removal of predators provided useful ancillary information for several species.

Rodents

The Franklin's ground squirrel—the only studied rodent—is a secretive species whose presence in an area may not be readily apparent. However, Franklin's ground squirrels are easily trapped (Choromanski-Norris 1983; Greenwood 1986) and, because they are diurnal, are occasionally seen. We used observation rates to rate abundance of Franklin's ground squirrels. Capture rates were also considered a reliable indicator of abundance but were not available for all study area-years. Moreover, observation rates reflected abundance throughout each study area, whereas capture rates reflected abundance in only the most dense brush and herbaceous habitats. Although observation rates did not increase with capture rates ($r = 0.33$, 21 df, $P = 0.129$) in study areas with both data types, Franklin's ground squirrels were captured in only two study area-years where they were not seen (different study areas, one in each area). Franklin's ground squirrels were seen in both areas in another year. Systematic livetrapping provided useful supplementary data on distribution in study areas and removal of predators provided useful ancillary data on abundance in some study areas.

Based on all collected data, descriptions of Franklin's ground squirrel populations by Sowls (1948), and observations of Franklin's ground squirrels elsewhere in the prairie pothole region (A. B. Sargeant, R. J. Greenwood, and M. A. Sovada, personal observations), we assumed only the highest rate of our observations indicated the abundance of the species could be categorized as numerous.

Corvids

Because of differences in nests and behavior of corvid species, we used different index methods to rate abundance of black-billed magpies and abundance of American crows and common ravens. The

average percentages of quarter sections in which they were detected during the road-transect counts were the primary data used to rate abundance of black-billed magpies. Those data were augmented with observation rates and with incidental records of occupied nests. Based on literature (Brown 1957; Shaw 1967) and our findings, we assumed the highest index value we obtained indicated the abundance of the species could be categorized **numerous**. In study areas where black-billed magpies were not detected during counts along road-transects and in study areas where counts along road-transects had not been made, we categorized the abundance of these birds **undetected** if they were not seen, **scarce** if they were seen at ≤0.005 place/ h, and **uncommon** if they were seen more often.

The primary data for rating abundance of American crows were the density of occupied nests. The data on density were supplemented with information from the road-transect counts and observation rates.

We estimated numbers of American crow nests in study areas in which no or partial nest searches were conducted from detection rates of American crows in quarter sections during the road-transect counts. The expansions were based on the relation between nest densities and average percentage of quarter sections in which they were detected (r = 0.91, 11 df, P <0.001) in study areas in Canada where both types of data were available. Based on literature (Kalmbach 1937) and on our findings, we assumed that a density of >0.58 occupied nest/km^2 was necessary to rate the species **numerous**. In areas without occupied nests, we rated American crows **scarce** if they were seen in ≤0.005 place/ h and **uncommon** if they were seen more often.

Common ravens were not initially included in our surveys because we presumed they would be absent, but our surveys of American crows in all searched study areas inadvertently revealed **common** abundances of ravens. We used the same criteria as for American crows to rate abundance of common ravens.

Raptors

We relied primarily on density of occupied nests to rate abundance of raptor species and, therefore, were unable to rate the abundance of raptors in the eight Central Flyway study areas where no systematic searches for nests and less overall field work was conducted. In searched study areas where no occupied nests of hawks were found, we rated each hawk species **undetected** if it was not seen, **scarce** if it was seen but was ≤5% of total sightings, and **uncommon** if it was >5% of sightings. In searched study areas where no nests of great horned owls were found, we rated the species **undetected** if it was not seen, **scarce** if it was seen in ≤0.005 place/h, and **uncommon** if it was seen more often. The difference in rating methods between hawks and the great horned owl was necessary because the observation rates of hawks were not species specific. No raptor species was rated **common** or **numerous** based on sightings alone.

We treated the 1983 data on nests of buteos in study areas in the prairie of Canada as complete counts, although no systematic searches for raptor nests were conducted during that year. In doing this, we assumed no buteo nests in study areas in the prairie of Canada were overlooked because of the conspicuousness of those nests and their tending adults, the limited wooded habitat available for nesting, and the extensive coverage by study personnel. We did not use the 1983 data on nests to rate abundance of buteos in study areas in the aspen parkland because some occupied nests were probably overlooked, especially in areas with considerable woodlands. After 1983, we assumed we found nearly all occupied nests of buteos in searched study areas because of the thoroughness of the searches. We used the same criteria to rate abundance of each buteo species. Based on the range of values from our and published information, we assumed a density of 0.08 occupied nest/km^2 was minimal to rate the abundance of a buteo species **common**.

No systematic searches for nests of northern harriers were conducted. However, rather than forgo rating the abundance of northern harriers, we assumed the intensity of searches for nests in the stabilized regulations and small unit management studies was comparable among study areas and that at least half of northern harrier nests were found opportunistically during the extensive searches for duck nests and monitoring of predators. We then treated the data on nest density as an index and rated the abundance of northern harriers on the same basis as the buteos, with a minimal index value of 0.08 occupied nest/km^2 to rate the species **common**. Although the proportion

of located nests by which we rated abundance was smaller for northern harriers than for other buteos, we believe the ratings are comparable with those for the buteos because northern harriers often cluster their nests (Bildstein and Gollop 1988). We assumed that high populations of northern harriers include more breeding pairs than high populations of the highly territorial buteos. We treated the data on nest density in study areas in the prairie and in the aspen parkland as equally complete because northern harriers seldom nest in woods (Stewart 1975; Bildstein and Gollop 1988).

With the same rationale we used for treatment of data about buteos, we treated the number of nests of great horned owls in study areas in the prairie of Canada in 1983 as complete counts and did not use such data from the aspen parkland in 1983 to rate the abundance of great horned owls. Because searches for raptor nests were conducted in late May and early June and great horned owls begin nesting in late February, about 6 weeks before other surveyed raptor species (Stewart 1975), nests of great horned owls were vulnerable to destruction (e.g., from weather or predators) for longer periods than nests of other raptors. To rate the abundance of great horned owls, we concluded 0.04 occupied nest/km^2 was minimal to rate the species common. However, nest densities of the great horned owl, as those of northern harriers, are indices.

Species Accounts

Carnivores

Coyote

Habitat and history. The coyote is adapted to prairie environments (Young and Jackson 1951; Andelt and Gipson 1979; Jones et al. 1983). Coyotes were distributed throughout the prairie pothole region before settlement (Young and Jackson 1951), but populations were low; in many areas they were less abundant than gray wolves (Bailey 1926). Gray wolves are antagonistic toward and reduce the abundance of coyotes (Mech 1970; Johnson and Sargeant 1977; Berg and Chesness 1978; Fuller and Keith 1981; Carbyn 1982). Coyote populations throughout the prairie pothole region increased substantially after settlement and after intensive control of the gray wolf (Bailey 1926; N. Criddle 1929; Bird 1930; Rand 1948b; Johnson and Sargeant 1977). By the early 1900's, coyotes were numerous in most areas (N. Criddle 1929; Williams 1946).

Coyotes prey on livestock, especially sheep, and on various game species (Bird 1961; Andelt 1987). As a result, coyotes throughout the prairie pothole region have been subjected to controls that include bounties, denning (killing pups at dens), shooting from aircraft, use of toxicants, and other methods (S. Criddle 1929; Bird 1930, 1961; Young and Jackson 1951; Adams 1961; Stoudt 1971; Johnson and Sargeant 1977; U.S. Fish and Wildlife Service 1978; Andelt 1987). Coyotes have also been extensively hunted and trapped for fur and recreation. Most mortality is inflicted by humans (Voigt and Berg 1987), and a strong case can be made that human-inflicted mortality has severely suppressed coyote populations in many parts of the prairie pothole region. The effect was greatest in intensively farmed areas in the southeastern portion of the region where coyotes were largely extirpated from many localities beginning about 1920 but especially after the 1940's (Johnson and Sargeant 1977). Control of coyotes continues in parts of the region but is less extensive than in the past, and coyotes are repopulating many areas from which they had been largely eliminated (A. B. Sargeant, personal observation).

Population structure. Coyote populations in spring are composed of family groups (generally a mated pair and one or more adult associates) and a few transients (Andelt 1985; Voigt and Berg 1987). Family groups occupy relatively discrete territories; home ranges of territorial individuals range from about 5 to 80 km^2 and include most of the family territory (Laundré and Keller 1984; Andelt 1985; Allen et al. 1987; Voigt and Berg 1987). Sargeant et al. (1987a) found that coyote territories in a low population in North Dakota averaged 61 km^2, whereas Roy and Dorrance (1985) found that coyote home ranges in a higher population in Alberta averaged 12 km^2. Home range size is inversely related to abundance and where coyotes are common or more abundant, all suitable habitat is included in coyote territories (Andelt 1985; Allen et al. 1987).

Distribution and abundance. Coyotes were present each year in all study areas except three in western Minnesota and two in eastern North Dakota, but abundance increased from southeast to northwest across the prairie pothole region (Fig. 5, Appendix Table 5). They were common or more abundant in a significantly greater percentage of study areas in Canada than in the United States (Appendix Table 6). In Canada, coyotes were numerous in 10 study areas (63%) and common in all others. In the United States, they were common in eight study areas (47%) and uncommon or less abundant in the others.

The percentage of study areas in which coyotes were common or more abundant did not differ between the prairie and aspen parkland (Appendix Table 7). However, the highest populations of coyotes were in study areas in the aspen parkland of Alberta and Saskatchewan (Fig. 5). Coyotes were numerous in all 8 study areas in that portion of the region, but in only 2 of the 25 other study areas. Coyotes were especially numerous in three

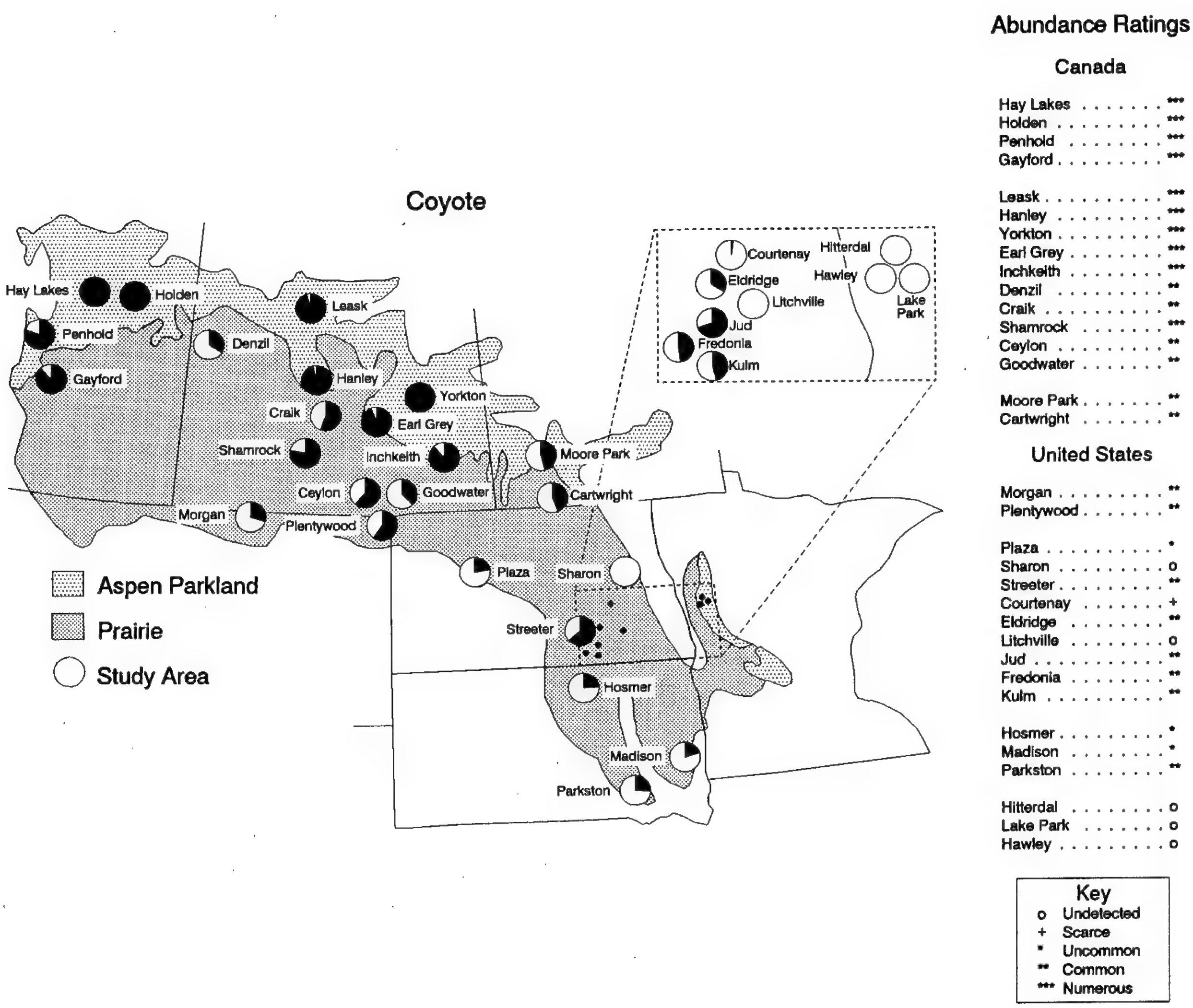


Fig. 5. Percentage of searched quarter sections (in *black*) by study area in which coyote tracks were found or in which the abundance of tracks was estimated during two systematic annual searches in April–June in ≥1 study year (Appendix Table 5) and ratings of the abundance of coyotes in each area, 1983–88. Results from study areas searched >1 year were averaged; study areas are in the prairie pothole region.

study areas (Hay Lakes, Holden, Yorkton) where their tracks were in all searched quarter sections (Appendix Table 5). Ten of 12 active rearing dens in study areas in Canada were in those three areas (Appendix Table 8). Five of the dens were in one study area (Hay Lakes) in 1984 and probably represented at least four coyote families. Those dens were widely spaced (nearest dens of neighboring coyote families were 3.2 km apart) and were simultaneously occupied by coyote pups. That number of active rearing dens in 26 km^2 indicated the population was very high and comparable to high-density populations reported elsewhere in North America (Andelt 1985). Only four coyote dens were found (all by aerial searches) in study areas in the United States.

Sargeant et al. (1987a) reported that coyote families in portions of North Dakota where coyote populations are low tend to center their activities in the most roadless areas, where cropland is least abundant. That pattern of occupancy was evident in several study areas, especially in the prairie of Canada where habitats of some study areas were divided between large blocks of intensively farmed cropland and portions of multi-section, largely roadless pastures (e.g., Ceylon, Goodwater). All portions of studied large multi-section pastures were occupied by coyotes; portions of study areas unoccupied by coyotes were always intensively farmed cropland. However, coyotes were present throughout several intensively farmed study areas (e.g., Earl Grey, Inchkeith), demonstrating the suitability of that habitat for occupancy. The apparent habitat-related differences in distribution of coyotes in individual study areas probably reflected differences in survival rates from human-inflicted mortality more than differences in habitat suitability.

Gray Wolf

Habitat and history. Gray wolves were abundant throughout the prairie pothole region before settlement but were largely extirpated by the early 1900's (Bailey 1926; N. Criddle 1929; Young and Goldman 1944; Soper 1946; Bird 1961; Carbyn 1984). However, gray wolves remained in the bordering forested zone where they continue to live (Banfield 1974; Carbyn 1982, 1984). Gray wolves occasionally invade the prairie and aspen parkland (Carbyn 1981, 1984) but have been unsuccessful in reestablishing viable populations. Gray wolves living near humans are highly vulnerable to human-inflicted mortality (Carbyn 1981, 1984; Fritts et al. 1985; Mech 1989).

Population structure. Gray wolf populations are generally composed of territorial packs of 3–20 or more individuals that often travel together and some lone and transient individuals (Mech 1970; Carbyn 1987). Average territory size of packs ranges from about 125 to >600 km^2 and is inversely related to population size (Carbyn 1987).

Distribution and abundance. Tracks of gray wolves were found only in one study area (Moore Park) in 1983 (Fig. 6; Appendix Table 5). The tracks were found during both searches and occurred in 4 scattered quarter sections in the eastern half of the area. Measurements of tracks indicated presence of one individual; species abundance was scarce. A landowner reported the occurence of gray wolves was not unusual in that area. The study area is 50 km south of the Riding Mountain National Park (2,944 km^2 forested wilderness enclave) where a population of gray wolves resides (Carbyn 1982, 1984).

Red Fox

Habitat and history. The red fox is adapted to prairie environments and to coexistence with humans (Sargeant 1982; Voigt 1987). Habitats throughout the prairie pothole region seem suited to this species, even though the geographic range of the red fox does not include portions of south-central Alberta and western Saskatchewan (Hall 1981). The red fox was sparsely distributed throughout the region before settlement and may have been less abundant than gray wolves or coyotes (Farley 1925; Bailey 1926). Red fox populations seemingly increased for a short time after settlement began (Seton 1909; N. Criddle 1929; S. Criddle 1929; Baines 1969; Sargeant 1982) but then declined. From the 1890's to mid-1930's, red foxes were scarce or absent throughout most of the region (Bailey 1926; S. Criddle 1929; Bird 1930, 1961; Soper 1946, 1961; Sargeant 1982). Beginning in the 1930's in the United States and in the late 1950's in Canada, red fox populations expanded greatly, especially in the eastern half of the region (Bird 1961; Dekker 1973; Johnson and Sargeant 1977; Stelfox 1980; Sargeant 1982; Jorgenson 1987).

Red foxes in the prairie pothole region have been subjected to the same human-caused mortality as coyotes but, in general, have not been affected as

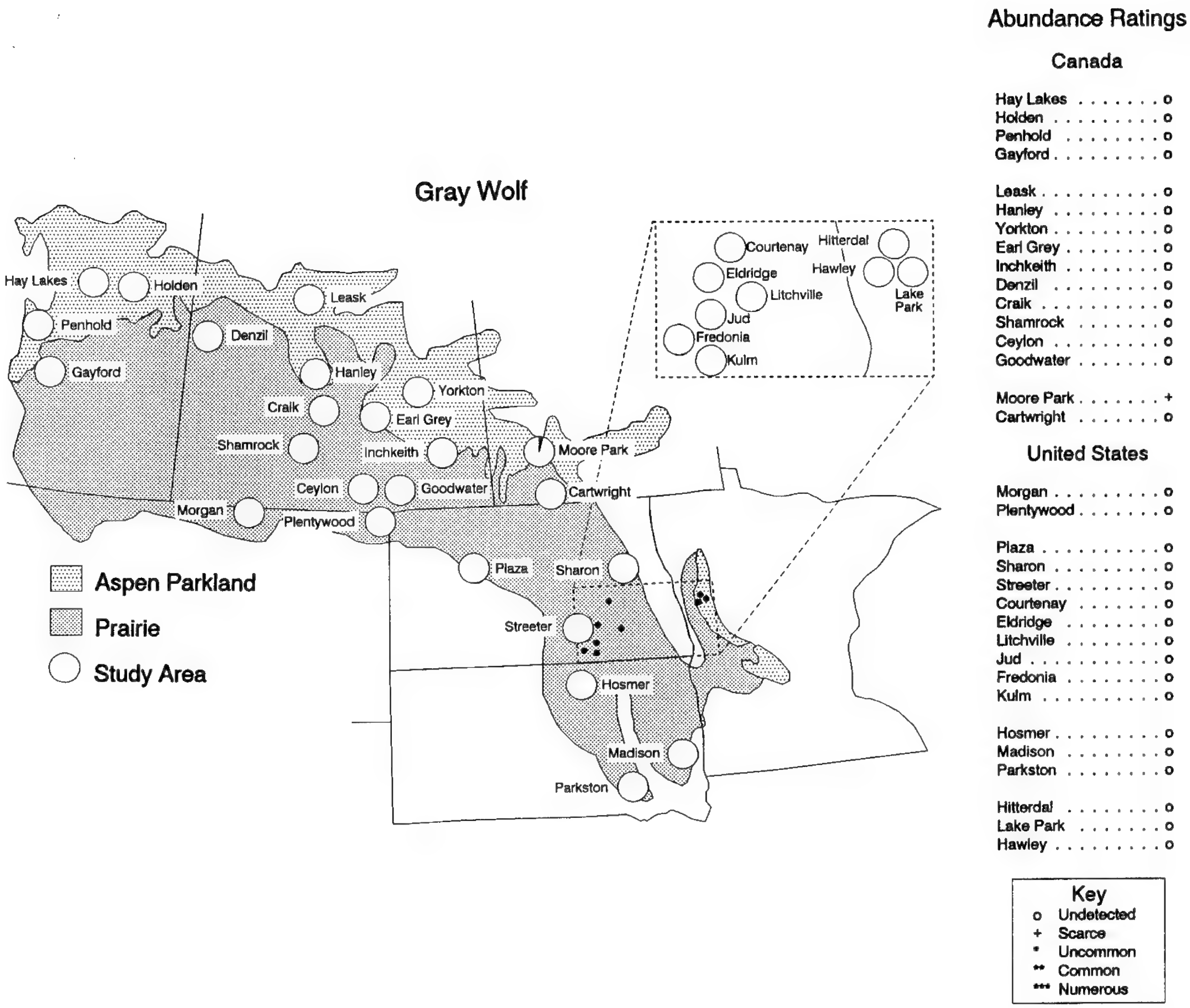


Fig. 6. Percentage of searched quarter sections (in *black*) by study area in which gray wolf tracks were found or or in which the abundance of tracks was estimated during two systematic annual searches in April–June in ≥1 study year (Appendix Table 5) and ratings of the abundance of gray wolves in each area, 1983–88. Results from study areas searched >1 year were averaged; study areas are in the prairie pothole region.

severely, probably because of differences in species biology. Red foxes tend to occupy much smaller home ranges than coyotes (individual foxes are exposed to fewer humans than individual coyotes), and red foxes have higher reproductive rates than coyotes. Most red foxes breed during their first year of life (Voigt 1987), whereas many coyotes do not breed until their second year (Voigt and Berg 1987). Nevertheless, during periods of exceptionally high fur pelt prices, human-inflicted mortality profoundly reduced abundance of red foxes in the region (Sargeant 1982).

Population structure. Red fox populations in spring are composed of family groups, usually a mated pair, but sometimes include additional adults (Sargeant 1972; Ewer 1973; Voigt and Macdonald 1984). Family groups occupy relatively discrete territories ranging from about 3 to 21 km^2 in rural areas but generally <12 km^2 (Sargeant 1972; Sargeant et al. 1987a; Voigt 1987; Trewhella et al. 1988). Territory size seems to be inversely related to population size (Sargeant 1972; Trewhella et al. 1988)). In the absence of coyotes, territories of red foxes tend to be contiguous and largely non-over-

lapping (Sargeant 1972; Voigt and Macdonald 1984; Mulder 1985). When coyotes are present, territories of red foxes tend to be discontinuous and around the periphery of territories of coyotes (Voigt and Earle 1983; Sargeant et al. 1987a).

Distribution and abundance. Red foxes were present each year in all except two study areas (Gayford; Hay Lakes in only 1984) in the western edge of the prairie pothole region (Appendix Table 5). The finding of up to nine rearing dens of at least four red fox families in individual study areas (Appendix Table 8) indicated that populations in several areas were comparable to the relatively high populations reported from other parts of North America and from portions of the prairie pothole region during other times (Sargeant 1972; Sargeant et al. 1975; Voigt 1987).

In general, the abundance of red foxes decreased from southeast to northwest across the region (Fig. 7). Red foxes were common or more abundant in a greater percentage of study areas in the United States than in Canada (Appendix Table 6) and in a greater percentage of study areas in the prairie than in the aspen parkland (Appendix Table 7). In

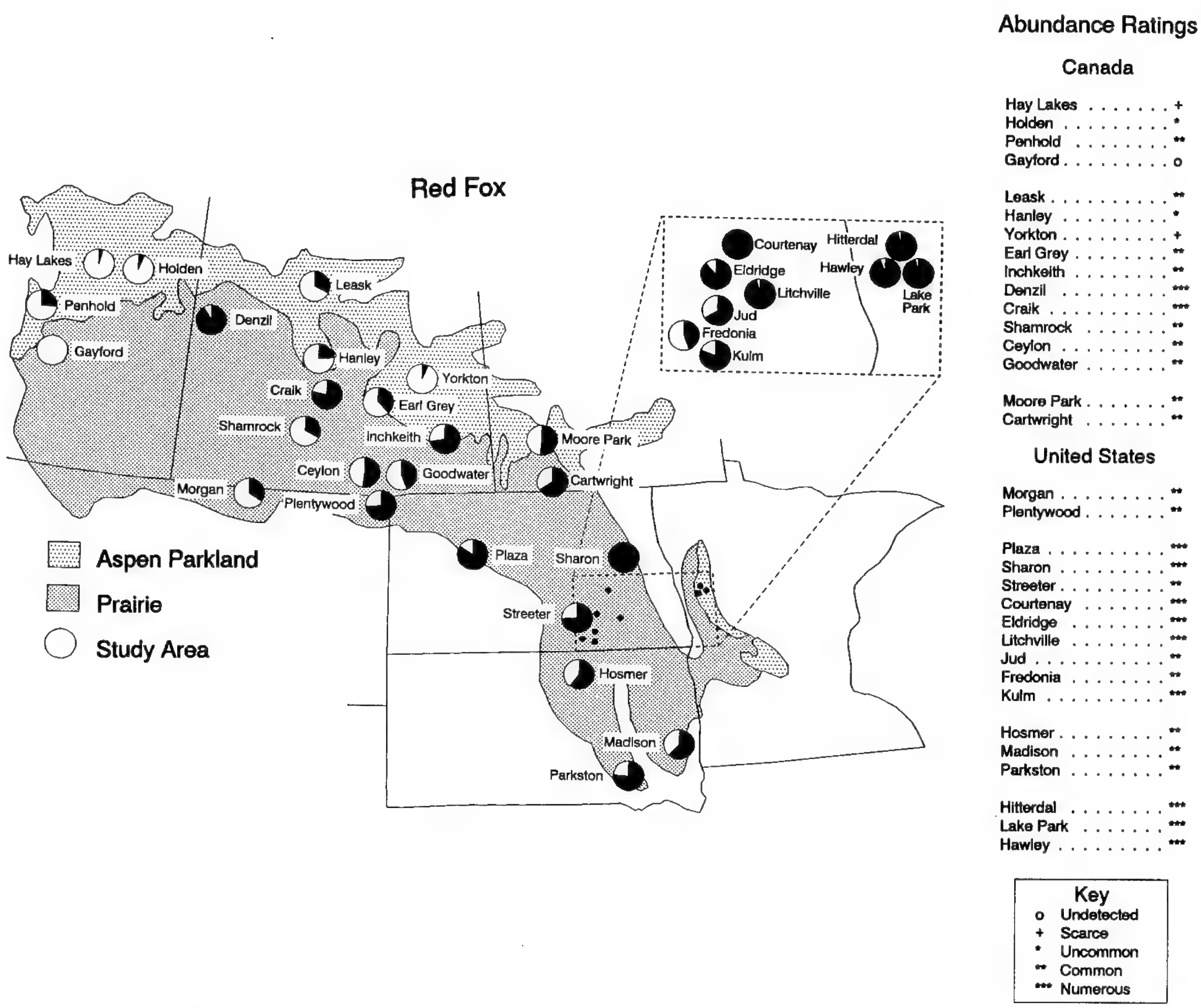


Fig. 7. Percentage of searched quarter sections (in *black*) by study area in which red fox tracks were found or in which the abundance of tracks was estimated during two systematic annual searches in April–June in ≥1 study year (Appendix Table 5) and ratings of the abundance of red foxes in each area, 1983–88. Results from study areas searched >1 year were averaged; study areas are in the prairie pothole region.

the United States, they were numerous in nine study areas (53%) and common in all others. In Canada, they were numerous in two study areas (13%), common in nine (56%), and uncommon or less abundant in five (31%). The removal of predators from three study areas (Eldridge, Fredonia, Lake Park) probably had no effect on the counts of red fox tracks. The first searches for tracks in those study areas were largely completed before any red foxes were captured, and tracks of red foxes continued to be found in quarter sections where trapping was conducted after red foxes were removed. Red foxes expand their territories to include adjacent areas soon after neighboring red foxes die (Sargeant 1972).

The highest indicated populations of red foxes were in study areas with the fewest coyotes (see section on Inter- and Intraspecific Interactions); these were also the most intensively farmed areas. Red foxes were especially abundant in study areas in western Minnesota and eastern North Dakota where they were numerous in 8 of 11 areas (Fig. 7). A notable exception to progressively fewer red foxes toward the northwest was one study area (Denzil) in western Saskatchewan where tracks were found in 88 and 97% of searched quarter sections during the 2 study years (Appendix Table 5). Of the study areas in Canada, this study area (Denzil) was one of the most intensively farmed (Table 1) and had one of the lowest coyote populations (Fig. 5).

Red foxes were absent from portions of many study areas in Canada, and in three of those study areas (Hay Lakes, Holden, Yorkton) tracks were found in only 2 or 3 quarter sections (Appendix Table 5), indicating occasional visits to a small part of each area. In most other study areas with tracks of red foxes in <50% of searched quarter sections, the quarter sections with tracks were clustered and often an active red fox rearing den was in one or more of the clusters (Hanley in 1984; Leask in 1984 and 1985; Penhold in 1985). Only one or two red fox families occupied portions of each of those study areas. The occupied quarter sections were always in intensively farmed areas and usually near farmsteads and well-traveled roads.

Raccoon

Habitat and history. Raccoons in the prairie pothole region are at the northern fringe of their geographic range (Hall 1981). At the time of settlement, raccoons were only in wooded hills and wooded river valleys in the southeastern portion of the region and were absent throughout nearly all of the region in Canada, except portions of southern Manitoba (Bailey 1926; N. Criddle 1929; S. Criddle 1929; Soper 1961; Kiel et al. 1972; Houston and Houston 1973; Cowan 1974). After settlement, raccoons became more widely distributed throughout the United States portion of the region, but populations in most areas remained low until the 1940's (Bailey 1926; Adams 1961). Thereafter, raccoons became relatively abundant throughout much of the southeastern portion of the region.

Beginning in the 1950's, raccoon populations in Canada began to expand (Sowls 1949; Santy 1958; Lynch 1971; Kiel et al. 1972; Houston and Houston 1973; Cowan 1974). During the 1960's, raccoons were sufficiently abundant in the Minnedosa area of southwest Manitoba (near the Moore Park study area) to be considered a major predator of clutches of canvasbacks (*Aythya valisineria*; Stoudt 1982). At that time, their presence was also noted near Redvers in southeastern Saskatchewan (Stoudt 1971) and near Delburne in south-central Alberta (Smith 1971). The latter observation seems inconsistent with other information on the occurrence of raccoons in Alberta and probably represented a localized population. Raccoon populations continue to expand in Canada (Friesen 1983; Jorgenson 1987).

The raccoon is highly suited to coexisting with humans and has benefitted greatly from agricultural development. Raccoons in the prairie pothole region make extensive use of buildings for resting and for rearing young (Cowan 1973; Fritzell 1978b) and make extensive use of cereal grains for food (Cowan 1973; Greenwood 1981). Principal causes of mortality in raccoons are killing by humans (especially trapping for furs and collisions with vehicles), disease (especially canine distemper), and starvation during winter (Mech et al. 1968; Lotze and Anderson 1979; Fritzell and Greenwood 1984; Clark et al. 1989).

Population structure. Raccoon populations in spring are composed of adult males, which may have large contiguous territories, and individuals of other age and sex categories. Home ranges of individuals of the latter groups are usually much smaller than those of adult males and may overlap considerably with those of conspecifics (Fritzell

1978a). In each adult male territory are usually one or more adult females and two or more yearlings, but many yearling males disperse from parent territories in mid- to late spring (Fritzell 1978a). Raccoon populations are much lower in the prairie pothole region than in many other parts of North America, and average home ranges are much larger than elsewhere (Lotze and Anderson 1979; Sanderson 1987). In North Dakota, home ranges of raccoons averaged 26 km^2 for adult males and 7–13 km^2 for individuals of other age and sex categories (Fritzell 1978a) but are generally <1 km^2 in other regions (Sanderson 1987).

Distribution and abundance. Raccoons were in all study areas except five in western sites, but abundance decreased from southeast to northwest across the region (Fig. 8). Raccoons were common or more abundant in a greater percentage of study areas in the United States than in Canada (Appendix Table 6). In the United States, raccoons were numerous in eight study areas (47%), common in eight (47%), and undetected in one (6%). In Canada,

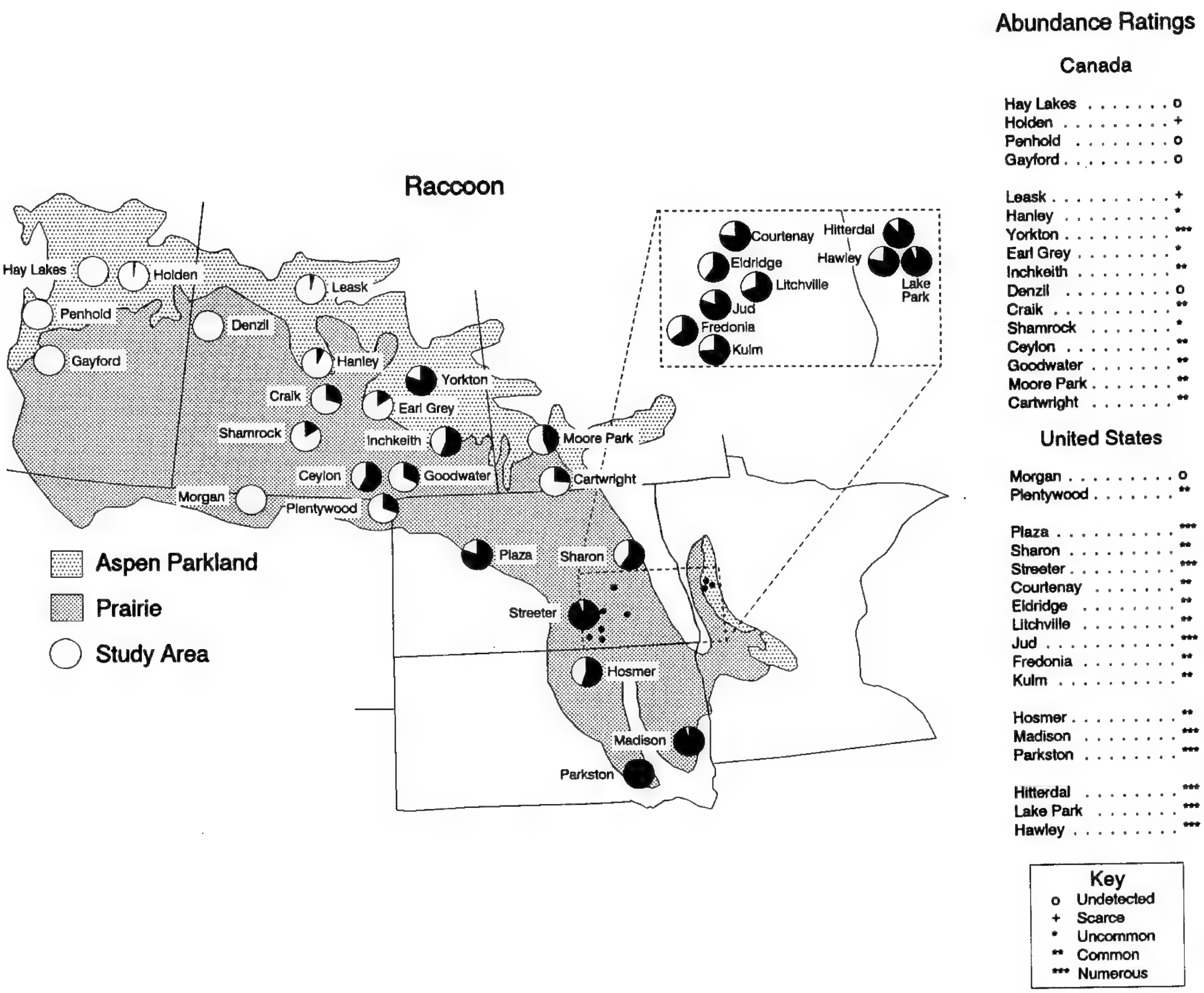


Fig. 8 Percentage of searched quarter-sections (in *black*) by study area in which raccoon tracks were found or in which the abundance of tracks was estimated during two systematic annual searches in April–June in ≥1 study year (Appendix Table 5) and ratings of the abundance of raccoons in each area, 1983–88. Results from study areas searched >1 year were averaged; study areas are in the prairie pothole region.

they were numerous in one study area (6%), common in six (38%), and uncommon or less abundant in nine (56%). Removal of predators from three study areas (Eldridge, Fredonia, Lake Park) probably had little effect on the track indices because only two raccoons were caught before the first searches for tracks were completed.

Seven of nine study areas with a numerous abundance of raccoons were in western Minnesota, eastern North Dakota, and eastern South Dakota (Fig. 8) where the climate is the most moderate and agriculture the most diverse in the region. Survival of raccoons probably benefits from these factors (Mech et al. 1968). In one of those study areas (Lake Park) 11 adult raccoons were captured in 1987 and 6 adults were captured in 1988 during predator removal (Appendix Table 3).

Raccoon populations in study areas in Canada were generally low or absent, especially in the western half of the region (Fig. 8). No evidence of raccoons was found in four of the five western-most study areas and raccoon tracks were found in only 1–4 quarter sections each year in three study areas (Hanley, Holden, Leask; Appendix Table 5). Deaths in these low populations affected track counts. In 1983, tracks were found in 18 quarter sections (45%) in one study area (Ceylon) during the first search period. Eight of those quarter sections were in a contiguous block that included an abandoned farmstead in its center. Between searches, three dead raccoons (an adult female and two kits) at the farmstead were seemingly killed by humans. During the second search, tracks were found in only 13% of quarter sections and no tracks were found in the 8 quarter sections with the abandoned farmstead. An exception to low raccoon populations in Canada was one study area (Yorkton), where raccoon tracks were found in 80% of quarter sections (Appendix Table 5). That area had more abandoned farm buildings suited for use by raccoons than any other study area in Canada.

Striped Skunk

Habitat and history. Striped skunks were distributed throughout the prairie pothole region before settlement but were most numerous in bushy or wooded areas (Seton 1909, 1953; Bailey 1926; Bird 1961; Kiel et al. 1972). They have remained widespread and generally common throughout the region although populations have fluctuated greatly in local areas (N. Criddle 1929; Banfield 1941; Soper 1946; Rand 1948b; Bird 1961; Wade-Smith and Verts 1982; Jones et al. 1983). Striped skunks are suited to living near humans but may not have benefitted greatly from habitat changes by agricultural development. They forage primarily on insects and use underground dens for rearing young and for dormancy in winter (Wade-Smith and Verts 1982; Rosatte 1987). Plowing destroys feeding areas and denning sites. Major causes of mortality are killing by humans, deaths in winter (e.g., starvation), and disease (Bjorge et al. 1981; Wade-Smith and Verts 1982). Striped skunks are easily trapped and large numbers are caught annually by fur trappers. Rabies is a major disease of striped skunks in the eastern two-thirds of the region. Rabies began spreading westward across the prairie pothole region of Canada in the late 1950's and prompted implementation of programs to eradicate striped skunks in some western areas (Tabel et al. 1974; Schowalter and Gunson 1982; Rosatte and Gunson 1984).

Population structure. Striped skunk populations in spring are composed of loose aggregations that often consist of an adult male and one or more adult females. Some adult males disperse to new areas in mid- to late spring (Sargeant et al. 1982). Home ranges of sexes overlap within and among social aggregations (Ewer 1973; A. B. Sargeant and R. J. Greenwood, unpublished data). Average home range sizes of adult skunks in the prairie pothole region range from 1.2 to 2.5 km^2 for females and from 2.9 to 3.1 km^2 for males (Bjorge et al. 1981; Rosatte and Gunson 1984; Greenwood et al. 1985).

Distribution and abundance. Striped skunks were in all study areas each study year (Appendix Table 5). The percentages of study areas with common or more abundant striped skunks did not differ between Canada and the United States (Appendix Table 6) and between the prairie and the aspen parkland (Appendix Table 7). Striped skunks were numerous in 6 (18%), common in 26 (79%), and uncommon in 1 (3%) study area (Fig. 9). Although they were captured (Appendix Table 9) and tracks were found (Appendix Table 5) in all study areas in Canada during all study area-years, we found no relation between capture rates of striped skunks and the percentage of quarter sections in which tracks of striped skunks were

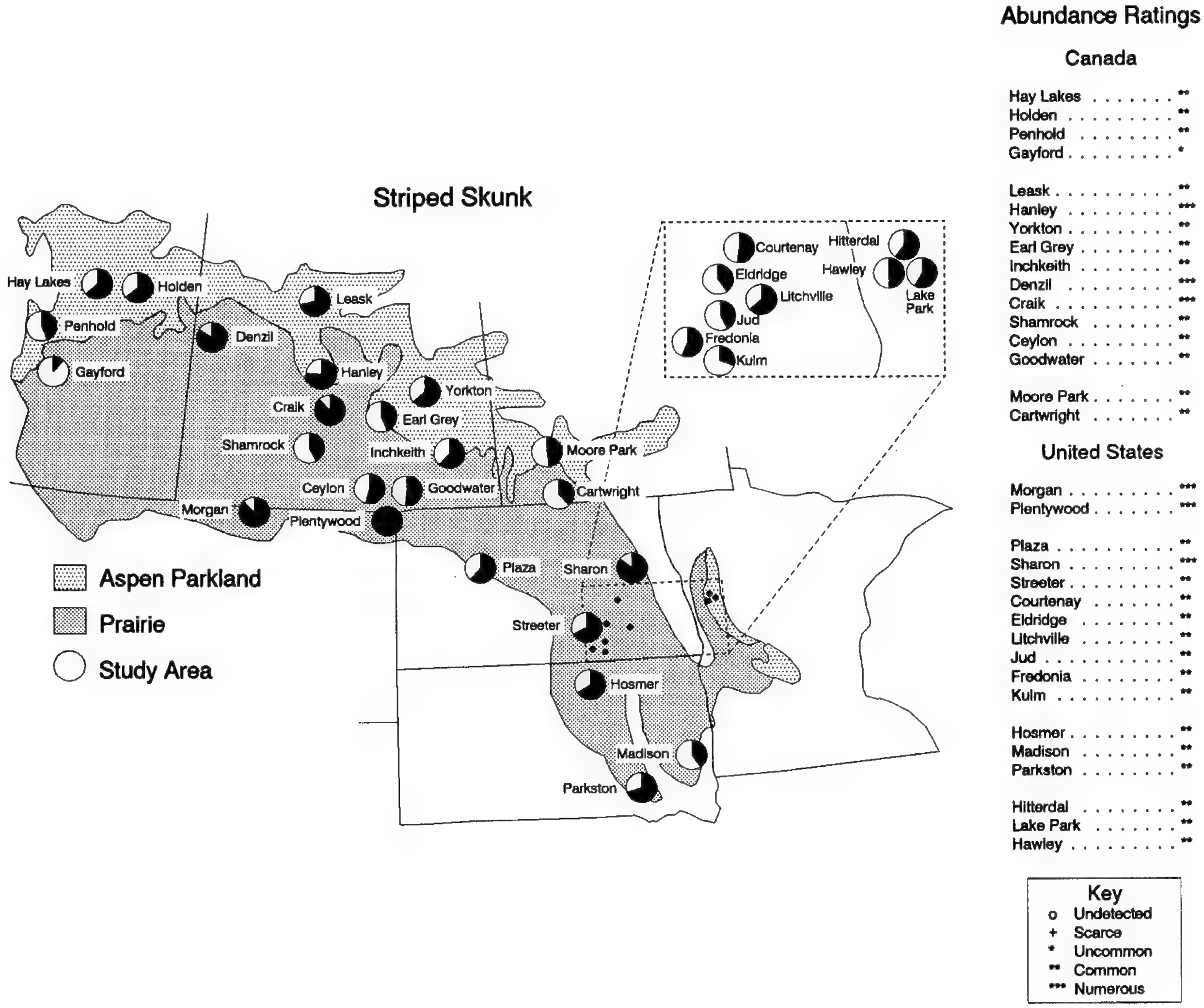


Fig. 9. Percentage of searched quarter sections (in *black*) by study area in which striped skunk tracks were found or in which the abundance of tracks was estimated during two systematic annual searches in April–June in ≥1 study year (Appendix Table 5) and ratings of the abundance of raccoons in each area, 1983–88. Results for study areas searched >1 year were averaged; study areas are in the prairie pothole region.

found ($r = 0.41$, 14 df, $P = 0.119$). (No livetrapping of striped skunks was conducted in study areas in the United States.) Variation in capture rates indicated differences in abundance were greater than revealed by the track index; populations were not high in any study area. The highest capture rate (0.125 per trap-night in one study area [Hanley] in 1985) was less than half that reported by Greenwood et al. (1985) for a study area in North Dakota where the density of adult striped skunks in spring was estimated to be between 0.5 and 1.0/km^2 (A. B. Sargeant and R. J. Greenwood, unpublished data). Densities of >5 striped skunks/km^2 were reported by many investigators (Rosatte 1987). The removal of 6–26 striped skunks annually from each of three study areas (Eldridge, Fredonia, Lake Park; Appendix Table 3) may have lowered the track indices. Captures and tracks of striped skunks were widely distributed in all except two study areas (Gayford, Earl Grey).

Badger

Habitat and history. Badgers in the prairie pothole region are near the northern edge of their geographic range (Hall 1981). They are adapted to northern grasslands and seemingly were abundant throughout the region at the time of settlement (Bailey 1926; Seton 1953; Bird 1961). Badgers have remained widely distributed throughout the region, but populations probably declined substantially after settlement and have remained low in most areas since that time (N. Criddle 1929; Soper 1946, 1961; Bird 1961; Baines 1969; Banfield 1974; Jones et al. 1983).

The badger has not benefitted from human presence. It was intensively trapped for fur during the early 1900's and populations throughout the prairie pothole region were greatly reduced (Bailey 1926; Bird 1930; Drescher 1974; Jones et al. 1983). Moreover, it was often killed directly by humans because it dug unwanted holes and indirectly by collisions with vehicles (Messick et al. 1981). The reproductive potential of badgers is low (Messick 1987); hence, population levels are easily reduced by high mortality. Habitat changes in the region have also harmed this species. Badgers are fossorial and feed extensively on small rodents, especially ground squirrels (*Spermophilus* spp.) and pocket gophers (*Geomys bursarius*, *Thomomys talpoides*; Salt 1976; Messick and Hornocker 1981; Jones et al. 1983). Extensive conversion of grassland to cropland greatly reduced the availability of this prey. Badgers are particularly noticeable because of their digging, but finding identifiable tracks in areas with low badger populations is often difficult.

Population structure. Adult badgers are solitary although home ranges of individuals may overlap considerably (Messick 1987). Home range sizes of adults averaged 1.6 and 2.4 km^2 for females and males in Idaho (Messick and Hornocker 1981) and ranged from 1.4 to 6.3 km^2 in Utah (Lindzey 1978). Home ranges of two radio-tracked females in Minnesota were 8.5 and 17.0 km^2 (Sargeant and Warner 1972; Lampe and Sovada 1981). The latter home ranges are probably more typical of badgers in the prairie pothole region.

Distribution and abundance. Badgers were present in all study areas except two (Hay Lakes, Hitterdal), but populations were low in most areas (Fig. 10). In general, badgers were most numerous along the southwestern edge of the region (where grassland is most abundant [Table 1]) and least numerous in the aspen parkland and in the most intensively farmed study areas (Fig. 10). The percentage of study areas in which badgers were common or more abundant was greater in the prairie than in the aspen parkland (Appendix Table 7); the difference was greatest of all surveyed carnivores. In Canada, badgers were common in 6 study areas (38%) and uncommon or less abundant in 10 (63%). In the United States, they were numerous in two study areas (12%), common in eight (47%), and uncommon or less abundant in seven (41%). In seven study areas, tracks of badgers were found in 1–3 quarter sections in a year, indicating intermittent presence of only one or two badgers in each area (Appendix Table 5). The removal of one adult badger from one study area (Fredonia) in 1987 and one from another (Lake Park) in 1988 (Appendix Table 3) probably lowered the index of badger tracks for those two study areas. The two adult badgers removed from one study area (Fredonia) in 1988 were caught after the track surveys were completed. The removal of only four adult badgers from the three areas from which predators were removed during 6 study area-years further suggested that populations were low.

Mink

Habitat and history. The prairie pothole region is in the center of the geographic range of the mink in North America (Hall 1981). Unlike the other studied carnivores, populations of this predator may not have been affected greatly by settlement (Bird 1961). Although minks are distributed throughout the region, they are not common everywhere or every year (Bailey 1926; Soper 1946, 1961). Minks depend on aquatic habitat. Rivers, streams, freshwater lakes, and deep marshes that contain prey such as fishes, crayfishes, and muskrats (*Ondatra zibethicus*) are preferred (Bailey 1926; Eagle and Whitman 1987). Minks also inhabit shallow prairie wetlands where their diet includes meadow voles (*Microtus pennsylvanicus*), waterbirds, aquatic insects, and tiger salamander (*Ambystoma tigrinum*) larvae (Eberhardt and Sargeant 1977; Arnold and Fritzell 1987b).

Minks that inhabit shallow prairie wetlands lead a precarious existence because annual fluctuations in water level affect abundance of food

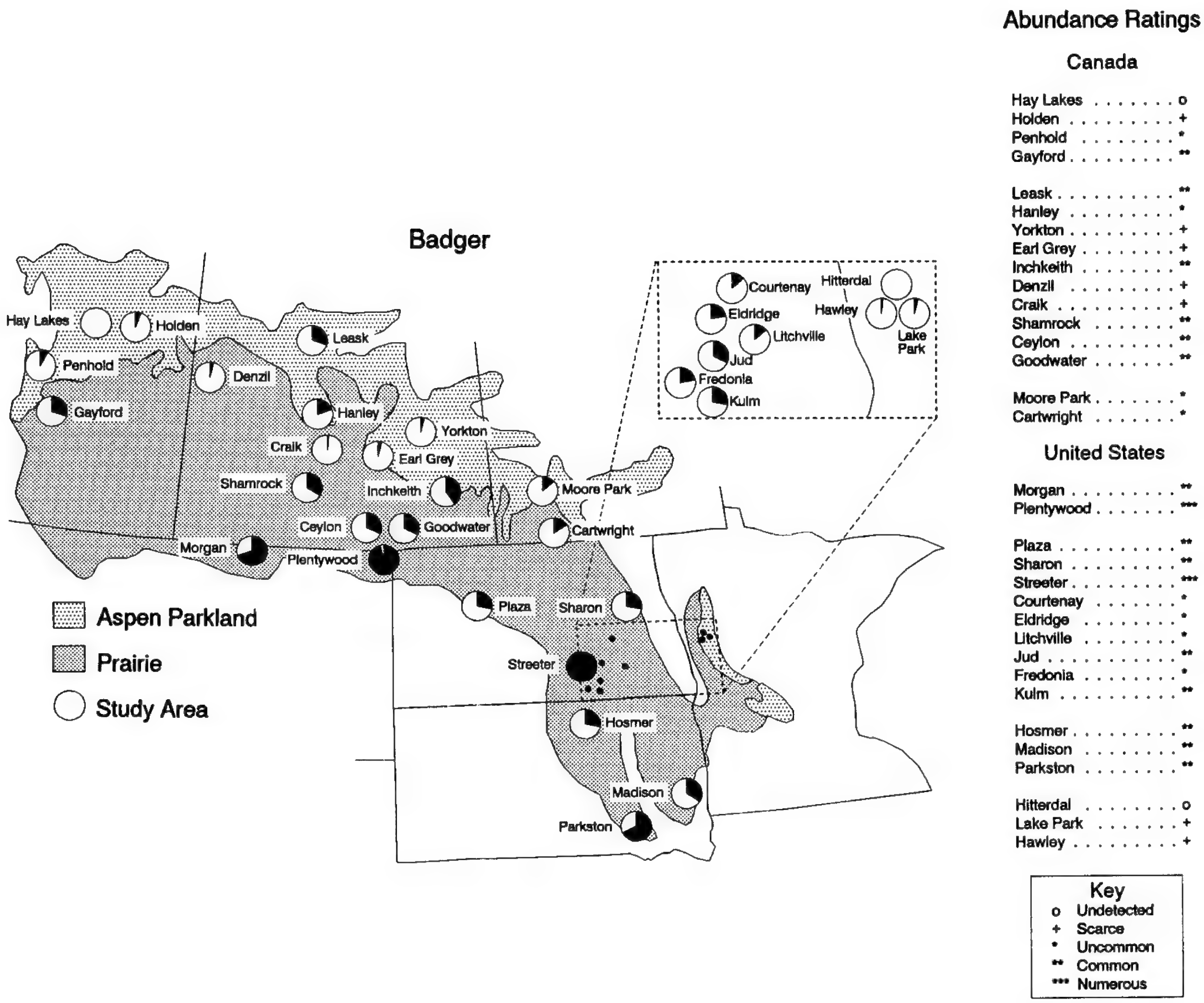


Fig. 10. Percentage of searched quarter sections (in *black*) by study area in which badger tracks were found or in which the abundance of tracks was estimated during two systematic annual searches in April–June in ≥1 study year (Appendix Table 5) and ratings of the abundance of badgers in each area, 1983–88. Results for study areas searched >1 year were averaged; study areas are in the prairie pothole region.

and availability of shelter. Frequent widespread and local droughts characteristic of the region lower reproductive performance by minks (Eberhardt 1974) and availability of prey. Shallow wetlands often freeze to the bottom during winter. The widespread severe droughts of the 1910's, 1930's, 1960's, and 1980's (Stoudt 1971; Kiel et al. 1972; Reynolds 1987) probably had catastrophic effects on the abundance of minks in the region.

Population structure. Mink populations in spring are composed of territorial males that occupy large areas and females that occupy small areas (Gerell 1970; Whitman 1981; Eagle and Whitman 1987; Eagle 1989). Nearly all studies of spacing and movements in minks have been in riverine, lacustrine, and coastal habitats where home ranges are best measured in terms of lengths of waterways or lengths of used shorelines rather than size of used areas. In prairie pothole habitat, minks tend to occupy circular home ranges that may encompass many wetlands. Arnold (1986) reported that home ranges of adult male minks during May through

July in pothole habitat of Manitoba (near the Moore Park study area) averaged 6.5 km^2 (range = 3.2–16.3 km^2) and included an average of all or parts of 285 wetlands. Female minks rearing kits seem to restrict their activities in spring to one or few wetlands (Eberhardt and Sargeant 1977; Eagle 1989).

Distribution and abundance. Minks were detected in only three study areas in Canada but were present in all nine small unit management study areas in the United States (Fig. 11). (No data on mink tracks were available from the eight Central Flyway study areas.) The percentage of study areas where minks were common or more abundant was greater in the United Stated than in Canada (Appendix Table 6). Mink tracks were found in all nine small unit management study areas each study area-year except in one (Eldridge) in 1987 (Appendix Table 5). In addition, minks were seen in all those study areas except one (Eldridge) during one or more study years (Appendix Table 10).

Although minks were not numerous in any study area, they were common in the three study areas

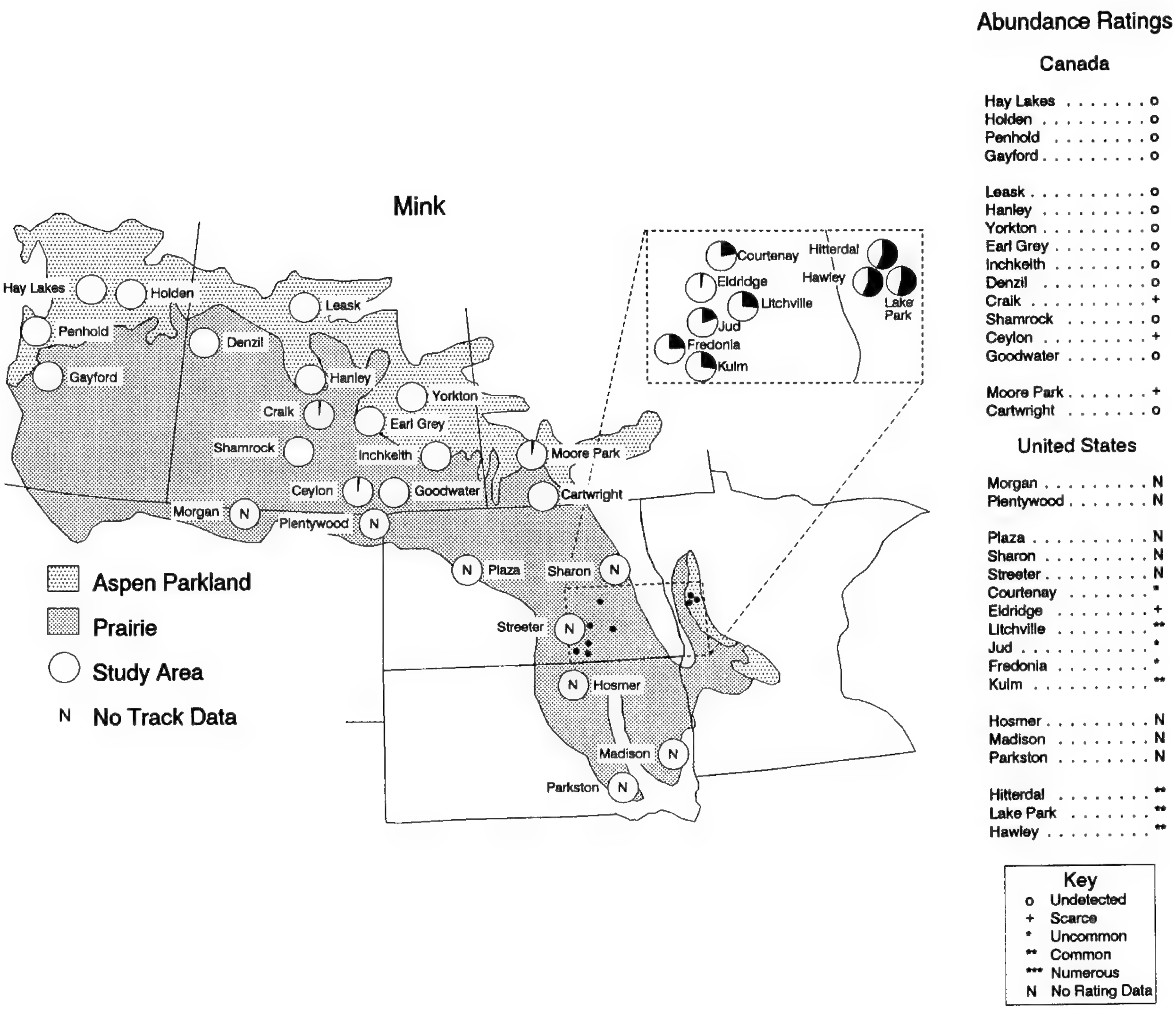


Fig. 11. Percentage of searched quarter sections (in *black*) by study area in which mink tracks were found or in which the abundance of tracks was estimated during two systematic annual searches in April–June in ≥1 study year (Appendix Table 5) and ratings of the abundance of minks in each area, 1983–88. Results for study areas searched >1 year were averaged; study areas are in the prairie pothole region.

in Minnesota and in two (Kulm and Litchville) in North Dakota. They were most common in the three study areas in Minnesota where their tracks were found in 43–67% of quarter sections searched each year and about twice as abundant as in any other area (Appendix Table 5). The relatively high abundance of minks in the study areas in Minnesota reflected favorable habitat that included numerous permanent wetlands and streams in and near each area.

The higher mink populations in small unit management study areas in North Dakota than in study areas in Canada (Fig. 11) probably reflected locations of study areas in the more temperate part of the prairie pothole region and selection of study areas. Although no data on mink tracks were collected in the Central Flyway study areas, no minks were observed in those areas during 3,468 observation-hours (Appendix Table 10), indicating low populations. Drought prevailed when those areas were studied. A criterion for choosing the small unit management study areas was that each should have many and diverse wetlands. One study area (Eldridge) with no mink sightings (Appendix Table 10) and the lowest mink track index of any small unit management study area (Appendix Table 5) had the fewest semipermanent wetlands of any such area.

In Canada, mink tracks were found in three study areas (Ceylon, Craik, Moore Park; Fig. 11). In each of those areas, the tracks were in only 1 or 2 adjoining quarter sections, indicating presence of a single mink; abundance in each area was scarce. No minks were seen in any study area in Canada during 23,954 observation-hours by field personnel (Appendix Table 10). Although minks were more difficult to detect than larger carnivores, we are confident that the data from Canada accurately portrayed populations in study areas as very low or absent. Many excellent sites for mink tracks were examined in each area. The drought and absence of rivers, continuously flowing streams, and permanent wetlands in most study areas probably contributed to the low mink populations.

Ermine and Long-tailed Weasel

Habitat and history. The geographic range of the ermine in the prairie pothole region is restricted primarily to the aspen parkland, whereas the range of the long-tailed weasel includes all of the region (Soper 1946; Rand 1948b; Banfield 1974; Simms 1979; Gamble 1981; Hall 1981). The long-tailed weasel is adapted to the prairie (Bailey 1926; Soper 1961; Jones et al. 1983). Population trends of the ermine and long-tailed weasel in the region are largely unknown, but seemingly both species were common during presettlement times (Bailey 1926; N. Criddle 1929). The extensive conversion of grasslands, wetlands, and woodlands to cropland must have reduced the abundance of weasels. The decline in harvest of long-tailed weasels in Saskatchewan from >60,000 pelts annually in the 1930's to <1,500 annually in recent years has been attributed largely to habitat changes (Fagerstone 1987).

Populations of weasels, especially ermines, fluctuate greatly in response to availability of food, especially small mammals (Gamble 1981). Population buildups of weasels occur periodically in the prairie pothole region and, because weasels are bold and curious mammals, such buildups should be evidenced by increased sightings.

Population structure. Adult male weasels seem to be intolerant of each other, except during kit-rearing (Jones et al. 1983), and occupy territories in which one or more females may reside (Ewer 1973; Fagerstone 1987). Home ranges of ermines and long-tailed weasels range from a few hectares to >1 km^2, depending on habitat type and food abundance; males occupy larger areas than females (Fagerstone 1987). Estimates of weasel densities in the prairie pothole region were not found, but estimates elsewhere range from about 4 to 6/km^2 for ermines and <1 to 38/km^2 for long-tailed weasels (Fagerstone 1987).

Distribution and abundance. All seen weasels were recorded as long-tailed weasels, but some were probably ermines, especially in the aspen parkland. Weasels were seen in 11 (69%) of the 16 study areas in Canada and in 9 (53%) of the 17 study areas in the United States (Fig. 12); sightings were infrequent in all areas (Appendix Table 10). Data were inadequate to rate abundance of weasels in individual areas. The maximum number of different annual sightings of weasels in study areas in Canada was four in one area (Hay Lakes) in 1983 and in the United States, seven in one area (Fredonia) in 1987. The abundance of meadow voles was noticeably high (seen daily during conduct of field work) in both of those study areas during those study years. Ten of 11 weasels

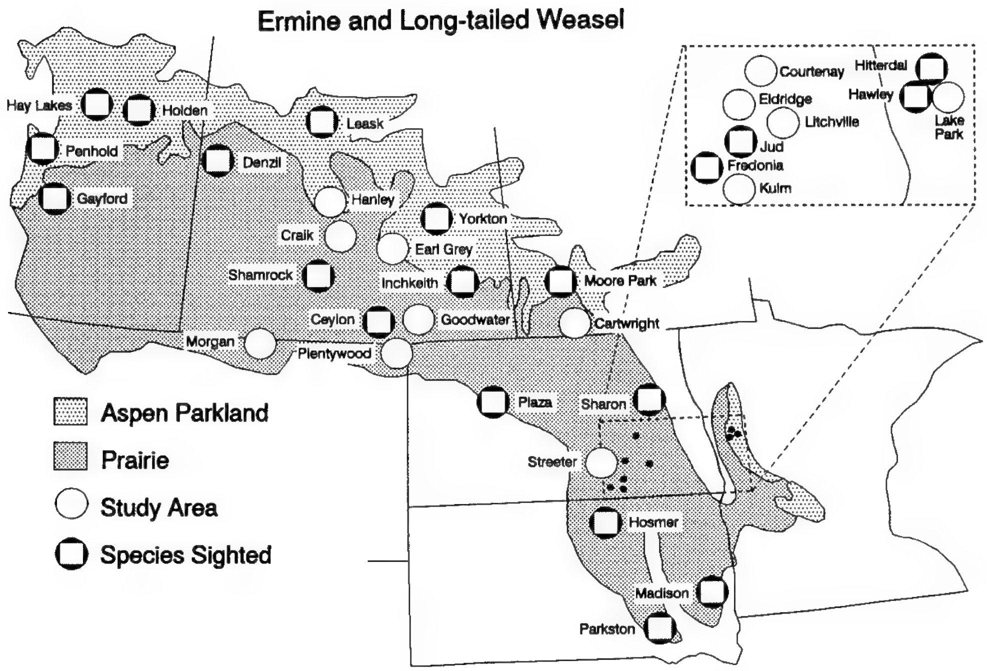


Fig. 12. Study areas in the prairie pothole region in which weasels (ermine and long-tailed weasels) were seen during annual surveys in the 1–3 years each area was studied, 1983–88 (Appendix Table 10).

caught during removal of predators from three small unit management study areas were from one area (Fredonia; Appendix Table 3).

Available information indicates weasels were rather uniformly distributed throughout the prairie pothole region and populations were low.

Rodents

Franklin's Ground Squirrel

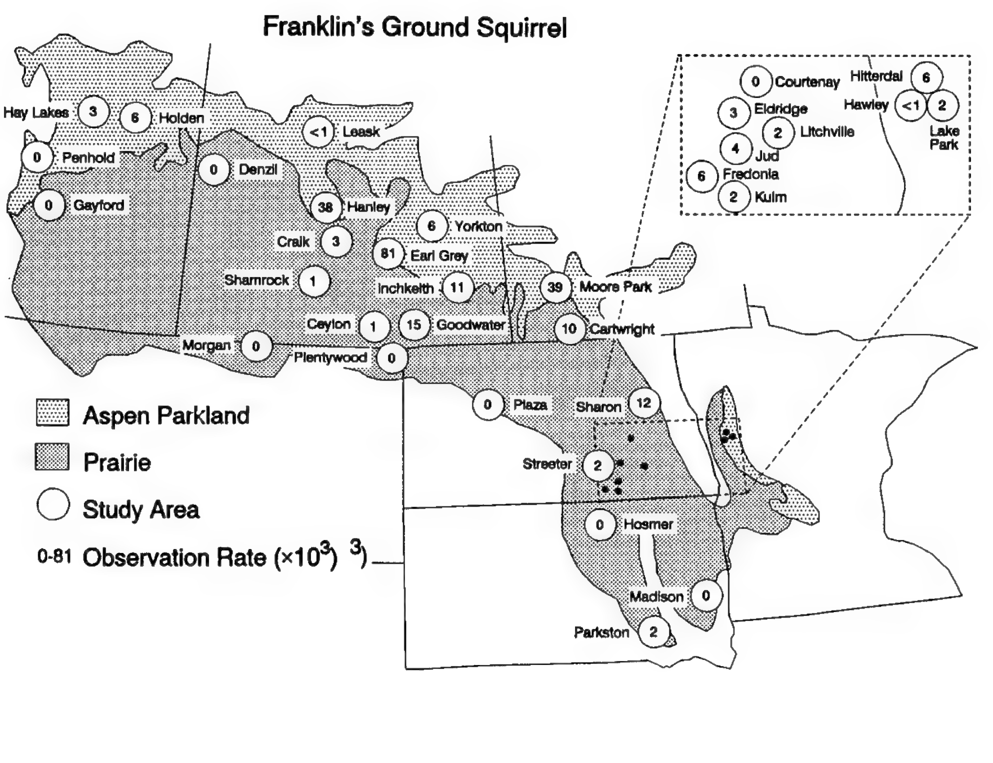
Habitat and history. The described geographic range of the Franklin's ground squirrel includes the eastern and northern portions of the prairie pothole region and excludes Montana, most of Alberta except the east-central portion, and southwest Saskatchewan (Banfield 1974; Hall 1981). Franklin's ground squirrels prefer bush and dense grass and herbaceous cover; they are seldom in habitats with sparse or short vegetation (Sowls 1948; Jones et al. 1983; Choromanski-Norris et al. 1989). Little is known about the abundance of this species before settlement or about population trends after settlement. However, because of its specific habitat requirements, Franklin's ground squirrels probably were scarce or absent throughout the prairie before settlement, except in locations with brush, and probably were numerous in the aspen parkland, except in western Alberta.

Agricultural development in the prairie pothole region has had both positive and negative effects on the distribution and abundance of Franklin's ground squirrels. Expansion of the aspen parkland created new habitat, whereas conversion of wooded and brush areas to cropland and intensive grazing by livestock reduced habitat. The establishment of farmsteads and tree plantings in the prairie created small parcels of suitable habitat and probably aided range expansion by this species. Banfield (1941) often saw Franklin's ground squirrels in the aspen parkland of central Saskatchewan in 1939. Soper (1946:141) found them "fairly common to abundant" in southwestern Manitoba during

1927–44 but "scarce or absent on the treeless prairies west of the Turtle Mountains."

Population structure. Adult Franklin's ground squirrels tend to be asocial although numerous individuals with overlapping home ranges may inhabit the same area (Choromanski-Norris 1983). Population densities in preferred habitat may fluctuate greatly (Sowls 1948); causes of fluctuations are largely undetermined. Densities of Franklin's ground squirrels are usually <2.5 adults/ha, although up to 12 adults and juveniles/ha have been reported (Sowls 1955; Murie 1973). In North Dakota, biweekly home ranges of Franklin's ground squirrels in dense grass and herbaceous cover averaged 7.4 ha for adult males and 2.8 ha for adult females (Choromanski-Norris et al. 1989).

Distribution and abundance. Franklin's ground squirrels were present in all but three study areas in Canada and in all but six study areas in the United States (Fig. 13). However, they were not caught or seen each year in each of those areas (Appendix Tables 10 and 11). Nearly all study areas in which they were undetected were along the western and southern edge of the region (Fig. 13). Popu-



Abundance Ratings

Canada

Hay Lakes	+
Holden	+
Penhold	o
Gayford	o
Leask	+
Hanley	**
Yorkton	*
Earl Grey	***
Inchkeith	*
Denzil	o
Craik	+
Shamrock	+
Ceylon	+
Goodwater	*
Moore Park	**
Cartwright	*

United States

Morgan	o
Plentywood	o
Plaza	o
Sharon	*
Streeter	+
Courtenay	o
Eldridge	+
Litchville	+
Jud	+
Fredonia	+
Kulm	+
Hosmer	o
Madison	o
Parkston	+
Hitterdal	*
Lake Park	+
Hawley	+

Key
- o Undetected
- + Scarce
- * Uncommon
- ** Common
- *** Numerous

Fig. 13. Observation rates of Franklin's ground squirrels by study area in the prairie pothole region (places seen per 1,000 h) during May–early July. Results from each study area are for ≥1 year, 1983–88 (Appendix Table 10); results from areas studied in >1 year were averaged.

lations were low in nearly all study areas where they were detected. The percentage of study areas where Franklin's ground squirrels were common or more abundant did not differ between Canada and the United states (Appendix Table 6). In Canada, Franklin's ground squirrels were numerous in one study area (6%), common in two (13%), and uncommon or less abundant in all others. They were uncommon or less abundant in all study areas in the United States. The capture and sightings of Franklin's ground squirrels in two study areas (Ceylon, Shamrock) represent small range extensions by this species (Beck 1958; Hall 1981).

The highest populations of Franklin's ground squirrels were in aspen parkland in the north-central portion of the prairie pothole region (Fig. 13). All three study areas where the species was common or numerous were in that portion of the region. The percentage of study areas where Franklin's ground squirrels were common or more abundant was greater in the aspen parkland than in the prairie (Appendix Table 7).

Populations of Franklin's ground squirrels were low in most study areas and individuals were patchily distributed. Differences in local abundance were large. For example, populations were highest and distribution was among the most uniform in one study area (Hanley; captures in 70–90% of sample units each year [Appendix Table 11]). However, in a nearby study area (Craik—65 km south of Hanley), Franklin's ground squirrels were not caught and were seen at only three places during the 2 study years. Although the latter area was more intensively cultivated than the former (Table 1), it contained many brush sites that seemed suitable for Franklin's ground squirrels. In the study area where the population was highest (Earl Grey), all captures and most observations of Franklin's ground squirrels occurred in the western 30% of the area. The population was much higher in those 7.7 km^2 than in any other comparably sized part of any study area; the population in the remainder of that area was low. In most other study areas, the captures of Franklin's ground squirrels indicated the species was restricted to small scattered habitat units. They were caught in ≥40% of the sample units in only four study areas (Appendix Table 11).

Further evidence of generally low populations of Franklin's ground squirrels was provided by the data on removal of predators from three study areas (Eldridge, Fredonia, Lake Park). Upland where trapping was conducted had dense grass and herbaceous cover with scattered patches of brush that is favorable habitat for Franklin's ground squirrels. Trapping of Franklin's ground squirrels was conducted continuously throughout May and June each year in each of the sites. Twenty-five Franklin's ground squirrels were removed from the three sites in 1987 during 1,654 trap-days and 11 in 1988 during 3,243 trap-days.

Corvids

Black-billed Magpie

Habitat and history. The black-billed magpie is a western North American species (Robbins et al. 1983; Godfrey 1986) that lives primarily in wooded and tall brush habitats, including farmsteads (Bent 1964; Shaw 1967; Bock and Lepthien 1975). The history of this species is discussed by many investigators (N. Criddle 1923; Farley 1925, 1932; Linsdale 1937; Rand 1948a; Houston 1949; Bird 1961; Houston 1977; Callin 1980). From these accounts, we concluded black-billed magpies were widely distributed and common throughout most of the prairie pothole region where tall brush and trees were available for nesting during the 1800's. By the turn of the century, black-billed magpies had become scarce or absent in much of the region but then gradually increased, especially after 1920 (Taverner 1926). The increases resulted in extensive attempts to control the abundance of the species (Phillips 1928; Salt and Salt 1976). Nevertheless, by the 1960's the black-billed magpie was common to abundant throughout the prairie pothole region of Saskatchewan (Houston 1977) and in western North Dakota and South Dakota (Stewart 1975; South Dakota Ornithologists' Union 1991). Although settlement of the prairie pothole region was initially detrimental to the species, the species seems to have benefitted from subsequent activities such as development of farmsteads (Salt and Salt 1976).

Population structure. Black-billed magpies tend to remain in the same area throughout the year and to live in loose colonies in which populations can build to high levels. Breeding densities of 24 and 28 birds/0.65 km^2 have been reported in

central Alberta and western Montana (Brown 1957; Shaw 1967).

Distribution and abundance. Black-billed magpies were much more numerous in study areas in Canada than in the United States (Fig. 14). They were common or more abundant in a significantly greater percentage of study areas in Canada than in the United States (Appendix Table 6). In Canada, they were numerous in 1 study area (6%), common in 5 (31%), and uncommon in 10 (63%). In the United States, they were detected in only three study areas (18%) and were scarce or uncommon in each. Although searches for occupied nests were not included in our surveys, nests with eggs or young were recorded during ≥1 year in all except four study areas in Canada (Gayford, Ceylon, Goodwater, Shamrock; Appendix Table 12). Occupied nests may have been present in one of those areas (Gayford) where birds were occasionally seen and nests could easily have been overlooked but were probably not present in the other three study areas where few birds were seen and nests would have been conspicuous. Most found nests were in active or abandoned farmsteads. No occu-

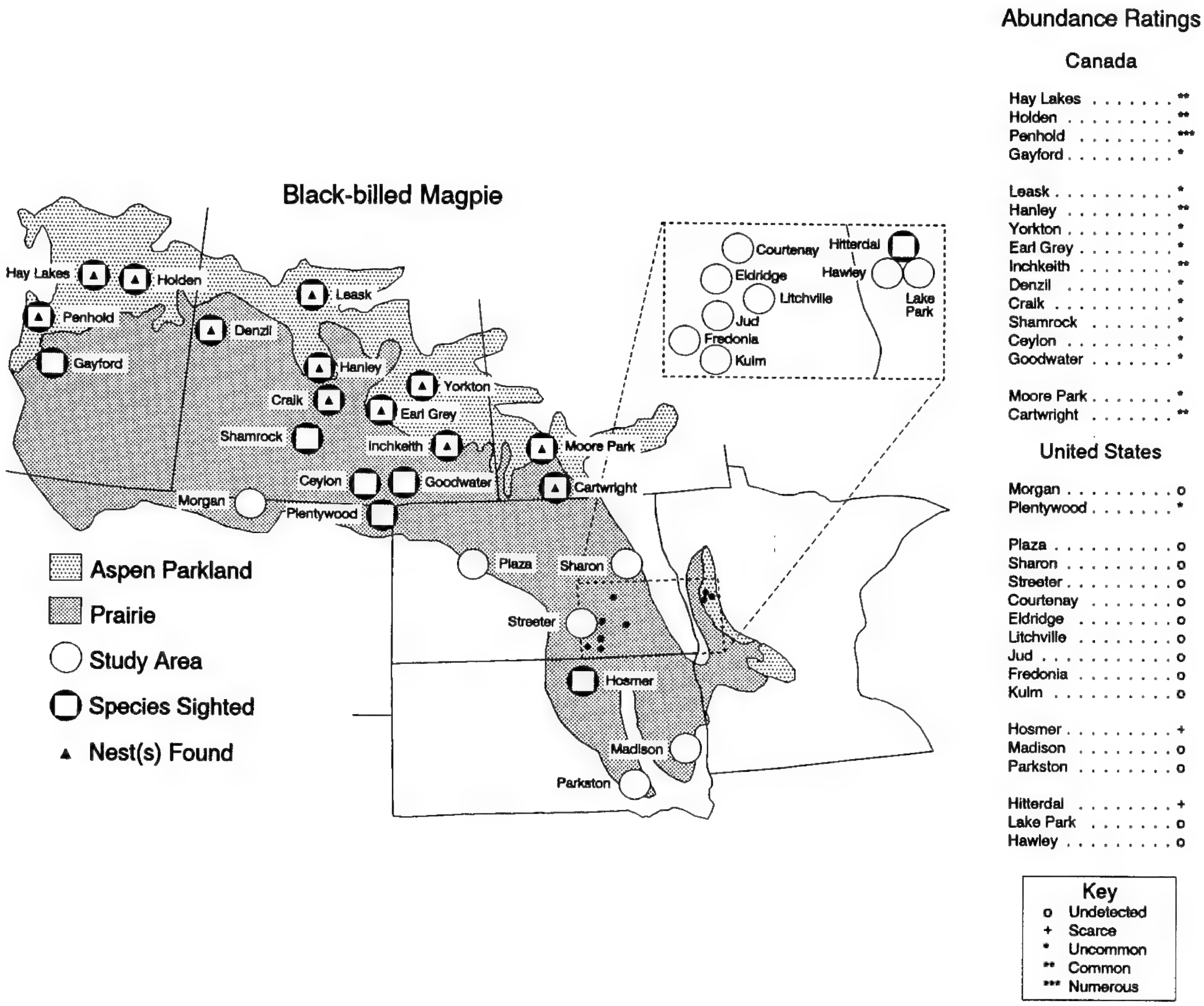


Fig. 14. Study areas in the prairie pothole region in which black-billed magpies were seen and occupied nests were found during annual surveys in the 1–3 years each area was studied (Appendix Tables 4, 12, and 13), and ratings of the abundance of black-billed magpies in each area, 1983–88.

pied black-billed magpie nests were found in any study area in the United States, but scattered breeding populations occur in that portion of the prairie pothole region (Stewart 1975).

Differences in abundance of black-billed magpies among study areas were particularly evident in Canada (Fig. 14; Appendix Tables 4 and 12). There, populations were greater in the aspen parkland (detected in an average of 3.1% [SD = 2.09] of quarter sections per road-transect count) than in the prairie (detected in an average of 0.9% [SD = 1.04] of quarter sections per road-transect count; $t = 2.5$, 14 df, $P = 0.025$). Populations were also greater in the west (detected in an average of 5.0% [SD = 2.20] of quarter sections per road-transect count in Alberta) than in the east (detected in an average of 2.2% [SD = 1.37] of quarter sections per road-transect count in Manitoba and Saskatchewan combined; $t = 2.4$, 7 df, $P = 0.047$). Notable exceptions were an uncommon abundance in one study area (Leask in aspen parkland) with abundant brush and wooded habitat and a common abundance in one study area (Cartwright in prairie) near the eastern edge of the region (Fig. 14).

American Crow

Habitat and history. The range of the American crow in North America includes all of the prairie pothole region (Rand 1948a; Stewart 1975; South Dakota Ornithologists' Union 1991). American crows were distributed throughout the region before settlement but were scarce or absent in most areas (Pittman 1928; Farley 1932; Bird 1961; Houston 1977). Populations expanded greatly after settlement (Taverner 1926; N. Criddle 1929; Johnston 1961; Houston 1977) and the species was abundant in much of the region by the 1930's (Hochbaum 1944; Sowls 1955; Bird 1961; Kiel et al. 1972; Houston 1977). Populations seemingly peaked in the 1940's but then began to decline (Bird 1961; Kiel et al. 1972). In North Dakota, the decline continued to the early 1980's (Rolandelli 1986).

Although the American crow benefitted greatly from agricultural development that provided trees for nesting and food (Schorger 1941), the species has been persecuted by humans. American crows have long been considered a major predator of clutches of ducks and other game birds (Taverner 1926), and efforts to reduce their numbers were widespread in many parts of the region during the 1920's to early 1950's (Todd 1947; Sowls 1955; Johnson 1964; Bihrle 1990). An estimated 100,000 American crows were killed in North Dakota during 1924 (Johnson 1964). In 1931 in Alberta, the Municipal District of Lloyd George paid bounties for 14,908 crow eggs and 924 pairs of crow feet (Farley 1932). The North Dakota Game and Fish Department sponsored annual statewide contests to control American crows in spring during the 1930's and 1940's and awarded prizes for the greatest numbers of destroyed birds and eggs (Anonymous 1941; Bihrle 1990). Ducks Unlimited sponsored extensive campaigns in the prairie pothole region of Canada and in 1944 reported that 760,238 adult birds and 982,697 eggs and nestlings had been destroyed during the previous 6 years (Anonymous 1944).

In 1972, the Migratory Bird Treaty Convention of 1936 between the United States and the United Mexican States was amended to include corvids (U.S. Fish and Wildlife Service 1975), thereby providing American crows with considerable protection in the United States. However, American crows remained unprotected in Canada (Godfrey 1986). Although organized campaigns to reduce the abundance of American crows were largely discontinued, hunting of the species in spring continues in many areas (Bihrle 1990).

Population structure. American crow populations in spring consist of adult breeding pairs, usually dispersed throughout an area but sometimes clumped, and yearling birds. Territorial behavior has been reported among neighboring groups (Kilham 1985). American crows seemingly first breed when 2 years old (Good 1952). Many yearlings seemingly return to their hatching locality (Good 1952) where they serve as helpers to breeding birds (Chamberlain-Auger et al. 1990). Flocks of nonbreeding adults may also be present throughout spring (Good 1952).

American crows can become very numerous. A population of breeding pairs, the density of which exceeded $0.62/km^2$, was reported for an area of approximately 31 km^2 in Saskatchewan in 1934 (Kalmbach 1937). Smith (1971:33) reported in Alberta, "Crow populations were occasionally censused throughout the parklands, and they were often larger than the local duck populations. It was not unusual to find 60 to 80 crows per square mile in prime duck habitat." Stoudt (1971:35) re-

ported in the Redvers area in aspen parkland of southeastern Saskatchewan "The crow population was very high from 1952 to 1957 and was estimated to equal that of the mallard, 45 pairs per square mile." Ignatiuk and Clark (1991) reported annual densities of 0.34–0.80 occupied nests/km^2 in three areas in the aspen parkland of Manitoba (near Moore Park) and Saskatchewan (between Hanley and Leask) during the late 1980's.

Distribution and abundance. American crows were observed (Fig. 15; Appendix Table 13) but did not nest (Fig. 15; Appendix Table 12) in all study areas. We observed mostly scattered breeding pairs but found a few clumped nests, several nesting sites where more than two adults were present, scattered individuals, and several groups of nonbreeders. American crows were common or more abundant in a significantly greater percentage of study areas in Canada than in the United States (Appendix Table 6). In Canada, they were numerous in 2 areas (13%), common in 13 (81%), and uncommon in 1 (6%). Occupied nests were in

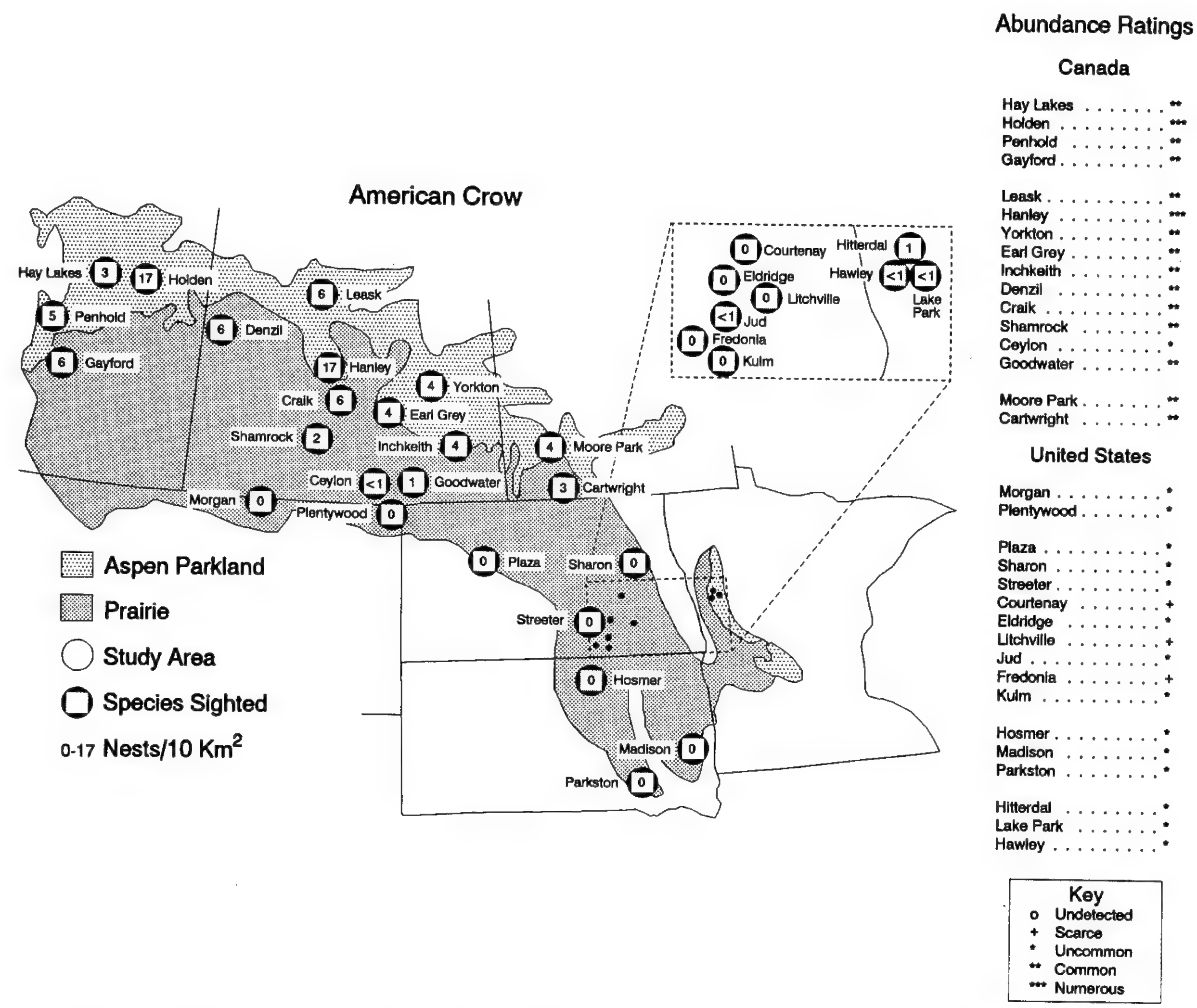


Fig. 15. Observed or estimated density of occupied nests of American crows (nests/10 km^2) in study areas in the prairie pothole region and ratings of the abundance of American crows in each area (rounding accounts for apparent discrepancies in ratings of the Gayford, Leask, Denzil, Craik study areas). Results for areas are for ≥1 year, 1983–88 (Appendix Table 13); results from areas surveyed in >1 year were averaged.

every study area in Canada each study area-year when thorough searches for nests were conducted; nest densities ranged from 0.1/km^2 in one study area (Ceylon) in 1984 to 1.9/km^2 in another (Hanley) in 1985 (Appendix Table 12). In the United States, American crows were uncommon in 14 study areas (82%) and scarce in 3 (18%; Fig. 15); occupied nests were found in five (29%) of the areas, including the nest found incidentally in one study area (Plentywood; Appendix Table 12). The highest density of nests in study areas in the United States was 0.09/km^2 (Hawley) in 1988. Thus, the lowest density of nests in study areas in Canada approximated the highest density in the United States.

In Canada, the largest populations were in study areas in the aspen parkland, especially two (Hanley, Holden) with 1.7 occupied nests/km^2 (Fig. 15). Counts of American crows along road transects also were highest in study areas in the aspen parkland. The average percentage of quarter sections in which American crows were detected per road-transect count in Canada was significantly greater in the aspen parkland (19.8% [SD = 12.23]) than in the prairie (11.8% [SD = 6.50]; t = 1.56, 14 df, P = 0.140). Both the lowest average densities of nests (Fig. 15) and the lowest average count along road transects (Appendix Table 4) were in the three southernmost study areas in Saskatchewan (in prairie). The average percentage of quarter sections in which American crows were detected per road-transect count in Canada did not differ between study areas in eastern (Manitoba and Saskatchewan) and western (Alberta) portions of the aspen parkland (17.5% [SD = 11.03] vs. 24.5% [SD = 15.65]; t = 0.79, 7 df, P = 0.453).

In the United States, the highest densities of American crows were in the aspen parkland of western Minnesota where four of six occupied nests were found or estimated present in study areas (Appendix Table 12). Behavior of American crows suggested four additional nests were in the study areas in Minnesota in 1987. The observation rates of American crows in small unit management study areas in Minnesota aspen parkland averaged 13 times the observation rates in small unit management study areas in North Dakota prairie (Appendix Table 13).

Common Raven

Habitat and history. Before settlement, the common raven was widely distributed in the prairie pothole region of Canada and was an occasional resident in portions of the region in the United States, but by the early 1900's, it was absent from nearly all of the region (Judd 1917; Potter 1943; Houston 1949; Stewart 1975; Houston 1977; South Dakota Ornithologists' Union 1991). The geographic breeding range of this species no longer includes the prairie pothole region but includes the adjacent forested region (Robbins et al. 1983; Godfrey 1986).

Population structure. Population structure and nesting behavior of the common raven are similar to those of the American crow; populations consist primarily of breeding pairs and nonbreeding yearlings (Bent 1964; Knight and Call 1980).

Distribution and abundance. Common ravens were seen in four study areas (Lake Park, Leask, Penhold, Yorkton) in the aspen parkland near transition forest (Fig. 16). They were seen regularly in one study area (Leask) where they were uncommon, and once each in the other three areas, where they were scarce; nests were not found.

Raptors

Northern Harrier

Habitat and history. The northern harrier has occupied all of the prairie pothole region since settlement (Robbins et al. 1983). It has probably always been the most abundant large hawk in the region, although populations seemingly have declined substantially during the last 20 years (Judd 1917; Taverner 1926; N. Criddle 1929; Bird 1961; Fyfe 1976; Whitney et al. 1978; Evans 1982). In North Dakota, northern harriers were the most abundant and widely distributed of all raptors in the late 1800's (Coues 1897); in the early 1900's Wood (1923) considered the species common in all parts of the state. Monson (1934:42) referred to northern harriers as a "Common summer resident, nesting two to four pairs to a section of meadowland" in an area about 8 km^2 in eastern North Dakota during 1925–32. Mitchell (1924) reported them common in southern Saskatchewan in the early 1900's. In southern Alberta, they were con-

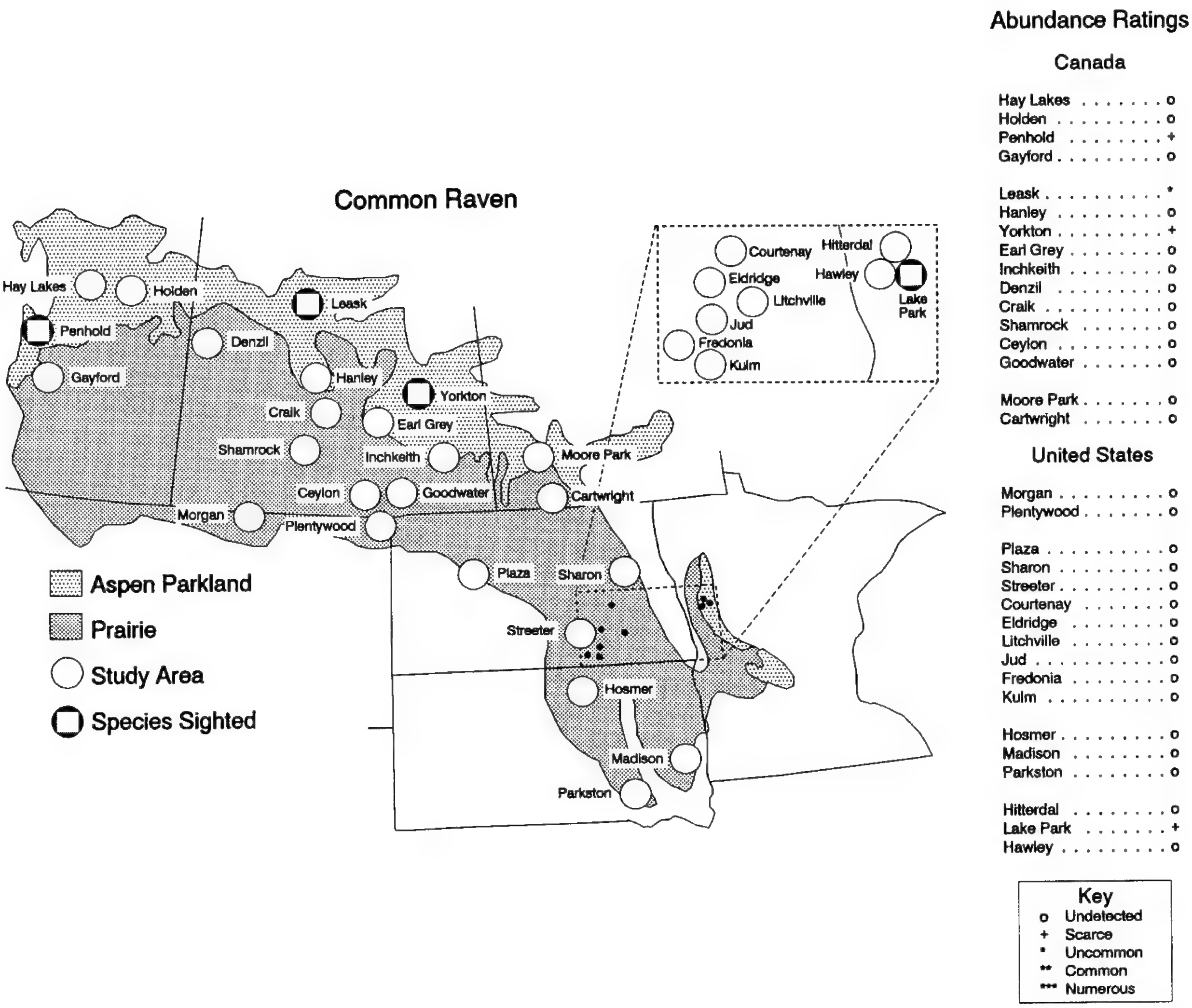


Fig. 16. Study areas in the prairie pothole region in which common ravens were seen during annual surveys in the 1–3 years each area was studied, 1983–88.

sidered abundant and the most common hawk in 1920 and were widely distributed but "hardly common" in 1945 (Rand 1948a:16). Farley (1932) also reported them to be common in south-central Alberta during the 1920's. Bird (1961) considered them the most abundant hawks in the aspen parkland before 1960 but stated they were less abundant than in earlier times. Todd (1947:393) reported northern harriers were "fairly common" in southern Saskatchewan in 1932. Fyfe (1976) categorized their abundance in the prairie provinces as low to medium during the mid-1970's. Stewart and Kantrud (1972) found them to be the most abundant hawks in North Dakota in 1967. However, Whitney et al. (1978) noted in South Dakota that, although northern harriers were one of the most numerous hawks, they were scarce in much of the eastern part of the state after 1966.

Habitat changes from agricultural development have been detrimental to the northern harrier (Evans 1982). Extensive drainage and cultivation and intensive grazing by livestock destroyed much nesting habitat of this species as well as much habitat of its principal prey species.

Population structure. The population structure of the northern harrier varies from spaced pairs to

groups of adults in loose nesting colonies of possibly polygamous individuals (Hecht 1951; Clark 1972; Hamerstrom et al. 1985). Breeding densities of northern harriers vary greatly in the prairie pothole region. Stewart and Kantrud (1972) estimated an average density of 0.19 pairs/km^2 throughout North Dakota during 1967. Lokemoen and Duebbert (1976), however, reported annual densities of only 0.02 and 0.01 pairs/km^2 in a 269-km^2 area in north-central South Dakota during 1973 and 1974. Sutherland (1987) found densities of 1.35 and 1.26 nests/km^2 on Mallard Island (11 km^2) in Lake Sakakawea, North Dakota, during 1984 and 1985, to which she referred as the highest reported densities in North America.

Densities of northern harriers in local areas often fluctuate greatly from year to year in response to availability of prey, especially meadow voles (Hamerstrom 1979, 1986). For example, Clark (1972) reported a density of about 3 nesting pairs in approximately 8 km^2 of the prairie pothole region in Manitoba during a year when meadow voles were scarce and at least 15 occupied nests in the same area the next year when meadow voles were abundant.

Distribution and abundance. Northern harriers were in all study areas each year (Appendix Table 14), but populations in most study areas were low (Fig. 17). In Canada, they were numerous in two study areas (13%), common in five (31%), and uncommon in nine (56%). In the nine study areas in the United States where abundance was rated, northern harriers were numerous in one (11%) and uncommon in eight (89%). The species composition data indicated that populations in the five Central Flyway study areas in Montana and North Dakota, in study areas in Manitoba and Saskatchewan, and in the small unit management study areas in North Dakota were similar (Appendix Table 14). The species composition data indicated that populations in the three Central Flyway study areas in South Dakota were lower than in most other study areas. The especially low incidence of northern harriers (2% of the sightings of large hawks) in one study area (Parkston) in South Dakota (Appendix Table 14) indicated near absence of the species. However, the percentage of study areas with common or more abundant (Appendix Table 6) northern harriers did not differ between Canada and the United States or between prairie and aspen parkland (Appendix Table 7).

Northern harriers were 2–76% of the sightings of large hawks annually in each study area and were the most commonly observed large hawks in 12 (36%) areas (Appendix Table 14). Populations in some areas studied >1 year varied greatly between years, seemingly in response to changes in availability of prey. The proportion of northern harriers among sightings of large hawks in one study area (Hay Lakes) declined from 45% in 1983 to 8% in 1984 (Appendix Table 14), concomitant with a decline from 4 to 0 nests (Appendix Table 15). The abundance of meadow voles (based on incidental sightings) was much greater in that study area (Hay Lakes) in 1983 than in 1984. Similar changes occurred in three other study areas (Ceylon, Craik, Moore Park) but could not be linked to apparent changes in abundance of meadow voles. In one study area (Fredonia), the number of occupied nests declined from 15 in 1987 to 3 in 1988 (Appendix Table 15), following an apparent decline in abundance of meadow voles; but the proportion of northern harriers in the sightings of large hawks remained the same (Appendix Table 14). A widespread severe drought began in 1988 and perhaps northern harriers returned to the area, but few nested.

Numbers of occupied northern harrier nests in individual study areas in a year ranged from 0 to 15 (Appendix Table 15); the greatest numbers were 14 (Goodwater) and 15 per study area (Fredonia). The meadow vole population seemed to be low in one area (Goodwater) but high in the other (Fredonia). The nests in the former were clustered with 13 of 14 in a 6.4-km segment (40%) of the area. In the latter, 14 of 15 nests (some may have been renests; Bildstein and Gollop 1988) in 1987 were in 3 km^2 of a Waterfowl Production Area. Another instance of clustering was near another study area (Hay Lakes) in 1983 where nine occupied nests were over water in cattails (*Typha* spp.) in a 31-ha wetland.

Swainson's Hawk

Habitat and history. The Swainson's hawk occurs in the western half of North America where it adapted to the prairie (Palmer 1988b). This hawk was widely distributed and probably the most abundant buteo in the prairie pothole region before

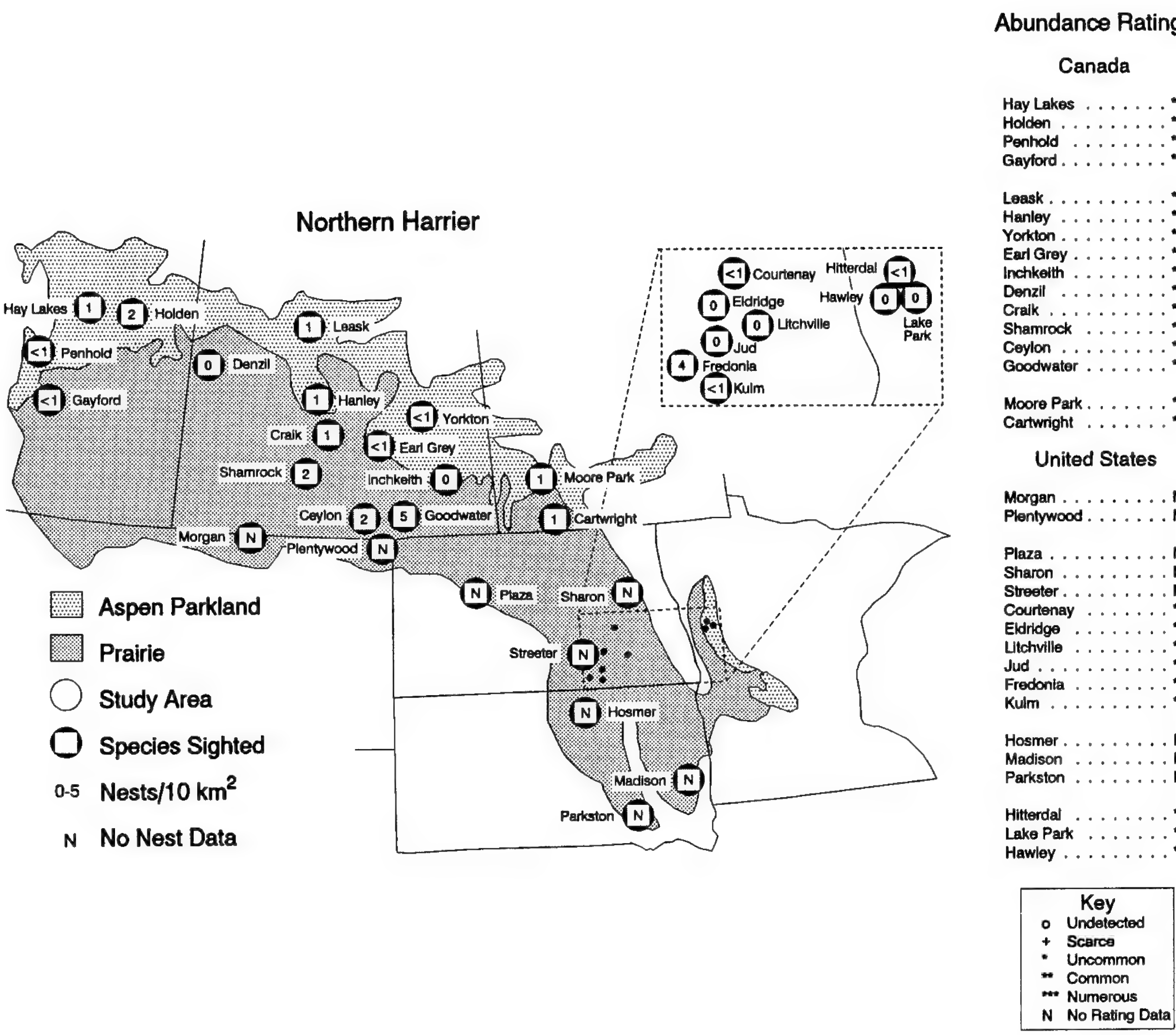


Fig. 17. Study areas in the prairie pothole region in which northern harriers were seen (Appendix Table 14), average density of occupied nests (nests/10 km^2) found incidentally in each area (Appendix Table 15), and ratings of the abundance of northern harriers in each study area. Results from each area are for ≥1 year, 1983–88; results from areas studied in >1 year were averaged.

settlement (Houston 1978; Houston and Bechard 1983). The extensive conversion of native grasslands to cropland and the expansion of the aspen parkland have altered nesting habitats and reduced habitat of the major prey species, especially Richardson's ground squirrels (*Spermophilus richardsonii*; Houston 1978; Bechard 1982; Gilmer and Stewart 1984; Houston and Bechard 1984; Schmutz 1989). Nevertheless, in Alberta, Schmutz (1989:368) found that "Swainson's hawks were largely opportunistic" and "preferred cultivated areas over grassland regardless of the extent of cultivation." Todd (1947:393) reported that Swainson's hawks were "common and generally distributed" in southern Saskatchewan in 1932, but Farley (1932:25) reported that in south-central Alberta, "the Swainson's hawk is not nearly as plentiful now as it was twenty years ago." Houston and Bechard (1983) presented convincing evidence that populations declined substantially in the aspen parkland of Saskatchewan. However, Schmutz (1984) found little evidence of a decline in Alberta.

Schmutz (1989) reported a 57% increase in the nesting population of Swainson's hawks from 1982 to 1987 in a study area in southeastern Alberta following an increase in abundance of Richardson's ground squirrels.

Swainson's hawks often nest in tall shrubs or low trees and are not averse to nesting near farmsteads or other areas of human activity (Schmutz et al. 1980; Gilmer and Stewart 1984; Schmutz 1984; Bechard et al. 1990). Because of these factors, their nests were particularly vulnerable to egg collectors during the early 1900's (Bechard and Houston 1984). Nests and adults were especially vulnerable to destruction (Cameron 1908; Judd 1917; Williams 1946); shooting hawks was a common practice until the 1950's (Farley 1932; Kirkpatrick and Elder 1951; Bird 1961; Salt and Salt 1976). These activities probably reduced the abundance of Swainson's hawks in the region (N. Criddle 1929).

Population structure. Swainson's hawks are strongly territorial and space their nests widely (Dunkle 1977; Schmutz et al. 1980; Rothfels and Lein 1983). Estimated densities of nests in several areas are available. Lokemoen and Duebbert (1976) found an average density of 0.004 occupied nests/km^2 in a 269-km^2 area in north-central South Dakota during 1973 and 1974. Gilmer and Stewart (1984) estimated an average density of 0.007 occupied nests/km^2 in a 16,519-km^2 area of south-central North Dakota during 1977–79. Schmutz et al. (1980) found an average density of 0.18 nesting pairs/km^2 in a 335–480 km^2 grassland area in southeastern Alberta during 1975–77, and Rothfels and Lein (1983) reported a density of 0.15–0.22 nesting pairs/km^2 in a 150-km^2 area in southwest Alberta during 1979–80. Schmutz (1984) estimated a density of 0.05 occupied nests/km^2 in the prairie region of Alberta in 1982.

Distribution and abundance. Swainson's hawks were present each year in all study areas except in western Minnesota (Fig. 18). The percentage of study areas with common or more abundant Swainson's hawks did not differ between Canada and the United States (Appendix Table 6). In Canada, they were common in seven study areas (44%) and uncommon in eight (50%). Abundance was undetermined in one (6%) study area (Holden) where four nests were found (Appendix Table 15). In the nine study areas in the United States where nests of raptors were censused, the abundance of Swainson's hawks was common in four (44%), uncommon in two (22%), and undetected in three (33%). The species composition data in the eight Central Flyway study areas from which no data on nests were available indicated the size of the populations there were similar to the size of populations in other study areas in the prairie (Appendix Table 14).

Swainson's hawks were common or more abundant in more study areas in the prairie than in the aspen parkland (Appendix Table 7). The three study areas in which they were not detected were in aspen parkland. Nest densities in completely searched study areas (excludes 1983 data) averaged 0.03 occupied nests/km^2 (SD = 0.04) in the aspen parkland, but 0.11 occupied nests/km^2 (SD = 0.05) in the prairie (calculated from data in Appendix Table 15). The highest density of occupied nests was 0.24/km^2 (six nests) in one study area (Ceylon) in the prairie in 1984 (Appendix Table 15).

There were notable exceptions to the pattern of highest densities of Swainson's hawks in study areas in the prairie. For example, in 1984 nest densities of 0.12/km^2 in two study areas (Hay Lakes, Inchkeith) in aspen parkland were the highest densities in any study area, but no occupied nests were in one study area (Cartwright) in prairie (Appendix Table 15). The high density of nests in the first area (Hay Lakes) was unexpected because it was one of the most heavily wooded areas (Table 1) and in the center of the aspen parkland of Alberta. The second study area (Inchkeith) had little woodland and was near the interface of the prairie and aspen parkland. Although no nests were in the third study area (Cartwright; Appendix Table 15), Swainson's hawk were frequently observed there (Appendix Table 14).

Swainson's hawks were 0–74% of the sightings of large hawks in study area-years and were the most commonly observed large hawks in 11 (33%) study areas (Appendix Table 14). All but one study area in which they were the most frequently seen hawks were in the prairie. Populations in areas studied >1 year varied little between years (Appendix Table 15). Occupied nests were widely spaced in all study areas; only once were two occupied nests within 0.8 km of each other.

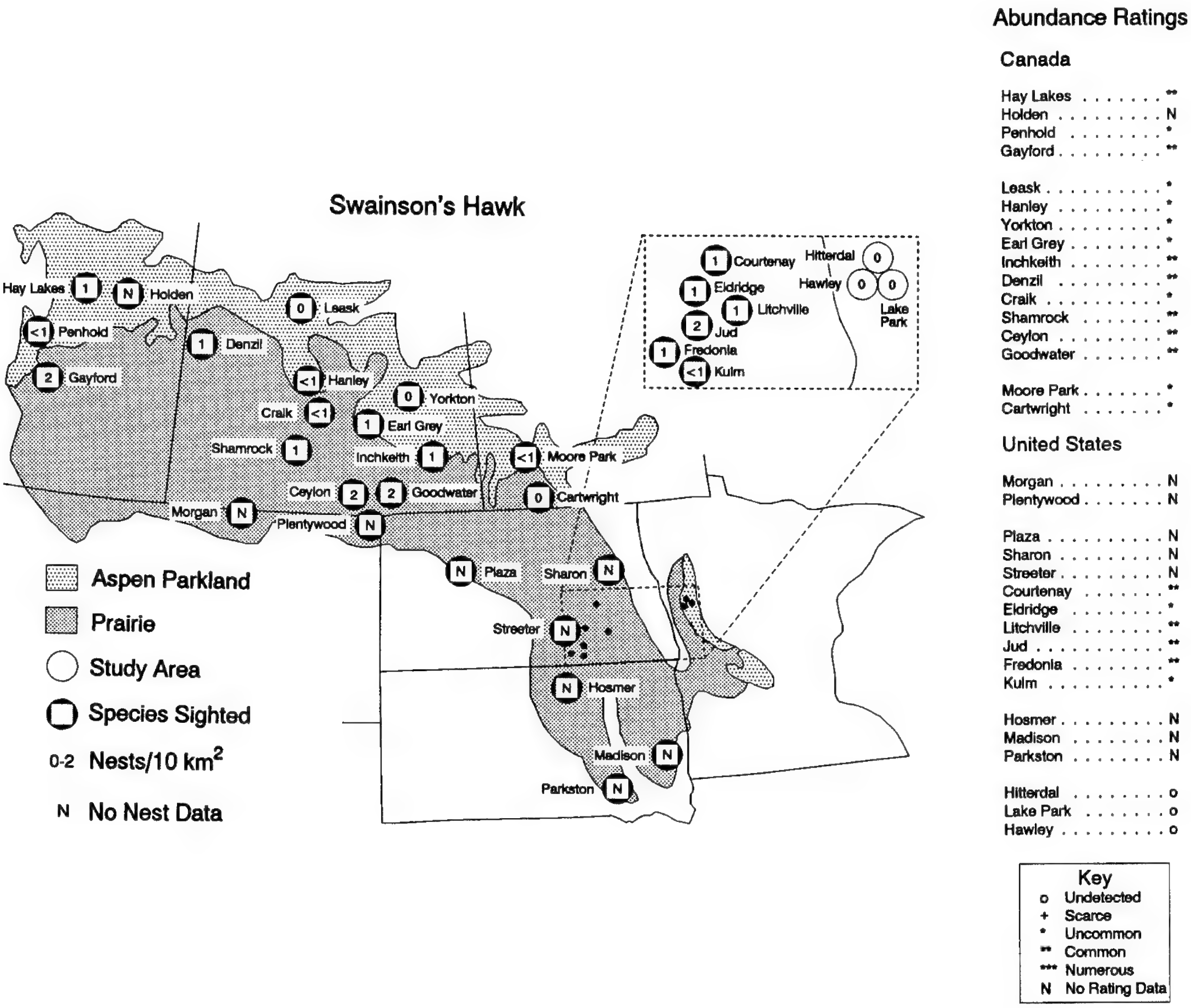


Fig. 18. Density of occupied Swainson's hawk nests (nests/10 km^2) in study areas in the prairie pothole region, and ratings of abundance of Swainson's hawks in each area. Results from each area are for ≥1 year, 1983–88 (Appendix Table 15); results from areas studied in >1 year were averaged.

Red-tailed Hawk

Habitat and history. The red-tailed hawk is distributed throughout most of North America and its present breeding range includes the entire prairie pothole region (Robbins et al. 1983; Godfrey 1986). This hawk is a woodland species that was scarce or absent throughout much of the region before agricultural development; it is the only studied large hawk that seems to have benefitted from agricultural development. The expansion of the aspen parkland zone and widespread planting of trees for windbreaks have favored this species (Houston and Bechard 1983). In Saskatchewan, Houston and Bechard (1983:105) concluded that "all evidence points to the red-tailed hawk being rare on the open plains, even in migration, until about 1920." As other hawks, the red-tailed hawk was subjected to indiscriminate shooting until the 1950's (N. Criddle 1929; Bird 1961; Salt and Salt 1976; Callin 1980). Presently, red-tailed hawks are considered at least common throughout the aspen parkland and are known to occasionally nest in the prairie where tall trees are present (Stewart 1975; Fyfe 1976; Lokemoen and Dueb-

bert 1976; Salt and Salt 1976; Houston and Bechard 1983).

Population structure. Red-tailed hawks are strongly territorial and tend to space their nests widely (McInvaille and Keith 1974; Rothfels and Lein 1983). Populations may include nonbreeding pairs and single birds (McInvaille and Keith 1974). Abundance tends to change little from year to year, and reuse of nests during successive years is high (McInvaille and Keith 1974; Adamcik et al. 1979).

Densities of red-tailed hawks in the prairie pothole region have been estimated. Adamcik et al. (1979) reported an average density of 0.12 breeding pair/km^2 during 1966–75 in a 162-km^2 area in the extreme northwestern portion of the aspen parkland in Alberta. In mixed aspen parkland–prairie, Schmutz et al. (1980) found 0.002 nesting pair/km^2 in a 335–480-km^2 area in south-central Alberta during 1975–77 (the pairs were in the most heavily wooded areas), and Rothfels and Lein (1983) reported a density of 0.42–0.47 nesting pair/km^2 in a 150-km^2 area in southwestern Alberta during 1979–80. In prairie habitat, Lokemoen and Duebbert (1976) found an average density of 0.004 occupied nest/km^2 in a 269-km^2 area in north-central South Dakota during 1973–74 and Gilmer et al. (1983) found an average density of 0.006 occupied nest/km^2 in a 1,259-km^2 area in south-central North Dakota during 1977–79.

Distribution and abundance. Red-tailed hawks were seen in all except six (Ceylon, Goodwater, Morgan, Plentywood, Shamrock, Streeter) study areas (Fig. 19) and were seen only once each study area-year in two (Fredonia, Plaza; Appendix Table 14). The eight study areas where none or only one hawk was seen annually formed a contiguous block along the west-central edge of the prairie pothole region (Fig. 19) and had the fewest trees (Table 1). In Canada, red-tailed hawks were numerous in two study areas (13%), common in six (38%), and uncommon or less abundant in seven (44%). Abundance was undetermined in one (6%) study area (Holden) but was at least common (four occupied nests were found [Appendix Table 15]). In the nine study areas in the United States where data on density of nests were collected, red-tailed hawks were common in two (22%), uncommon in six (67%), and scarce in one (11%). The species composition data from the eight Central Flyway study areas where data on nests were not collected, indicated absence or low populations of red-tailed hawks in nearly all areas (Appendix Table 14). The percentage of study areas with common or more abundant red-tailed hawks did not differ between Canada and the United States (Appendix Table 6).

Red-tailed hawks were common or more abundant in more study areas in the aspen parkland (includes Holden) than in the prairie (Appendix Table 7). Nest densities in study areas that were completely searched (excludes 1983 data) averaged 0.18 occupied nest/km^2 (SD = 0.19) in the aspen parkland and 0.02 occupied nest/km^2 (SD = 0.04) in the prairie (calculated from data in Appendix Table 15). The highest density of occupied nests in 1 year was 0.73/km^2 (19 nests) in one study area (Hay Lakes) in 1984 (Appendix Table 15) and was one of the highest recorded densities of the species in North America (Palmer 1988a). Eleven occupied nests were found in one study area (Hay Lakes) in 1983 during incomplete searches for nests. Only one study area (Hanley) in the aspen parkland had no nests. However, three occupied red-tailed hawk nests were found within 0.8 km^2 of that study area in both 1983 and 1984; no data from outside the study area were recorded in 1985. The near absence of red-tailed hawks from study areas in the south-central portion of the prairie pothole region (Fig. 19) is not representative of this entire portion of the region. For example, red-tailed hawks commonly nest in the Lostwood National Wildlife Refuge and in its vicinity (about 70 km north of the Plaza study area), where aspen parkland habitat invaded the prairie (R. K. Murphy, Lostwood National Wildlife Refuge, personal communication).

Red-tailed hawks were 0–91% of the sightings of large hawks in individual study area-years and the most commonly observed large hawks in nine (27%) study areas, all of which were in the aspen parkland (Appendix Table 14). Populations in areas studied >1 year seemed to be stable except in one study area (Penhold) where the number of occupied nests declined from seven in 1984 to two in 1985 (Appendix Table 15). Two nests there in 1984 were in quarter sections that could not be searched in 1985 (access denied). Remains of two dead red-tailed hawks were found in this study area in 1985 near nests that were occupied in 1984

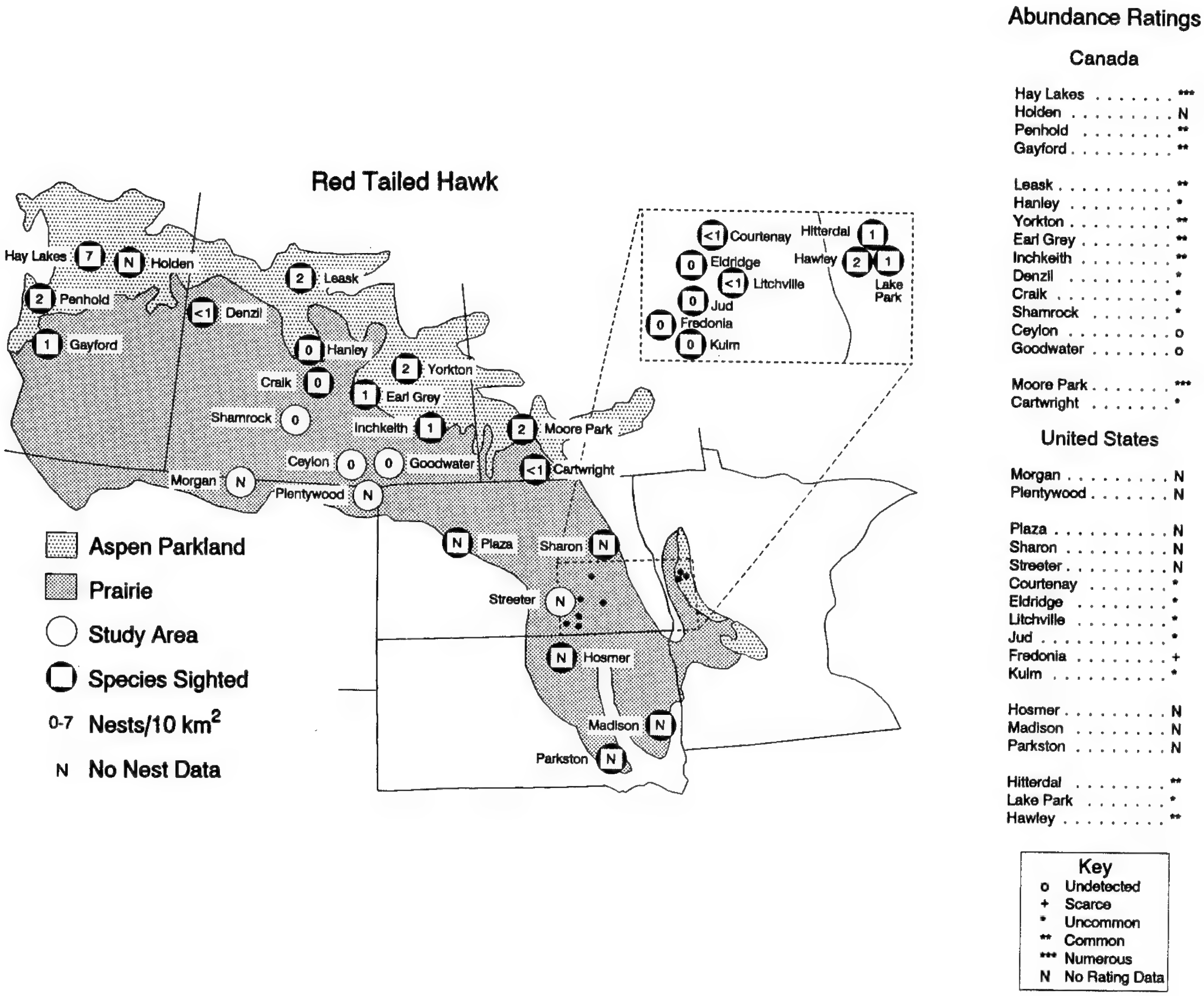


Fig. 19. Density of occupied red-tailed hawk nests (nests/10 km^2) in study areas in the prairie pothole region, and ratings of abundance of red-tailed hawks in each area. Results from each area are for ≥1 year, 1983–88 (Appendix Table 15); results from areas studied in >1 year were averaged.

but not in 1985. The mortality, possibly human-inflicted, reduced the number of breeding pairs.

Ferruginous Hawk

Habitat and history. The breeding range of the ferruginous hawk, one of several species that characterize the avifauna of the mixed-grass prairie (Stewart 1975), includes most of the semi-arid plains of west-central North America (Robbins et al. 1983). The ferruginous hawk was common throughout the prairie pothole region before settlement, but populations declined after settlement; presently it is scarce or absent in much of the region (Wood 1923; Stewart 1975; Callin 1980; Bechard 1981; Houston and Bechard 1984; Schmutz 1984; Smith 1987). Williams (1946) reported that ferruginous hawks were locally common in southern Alberta and southwestern Saskatchewan during 1923–26, and Todd (1947:393) reported that they were still "fairly common (for a bird of prey)" in southern Saskatchewan in 1932. Several factors that harmed this hawk included extensive collecting of eggs (Bechard and Houston 1984), indiscriminate shooting, expansion of the aspen parkland,

and plowing of grasslands. The latter destroyed nesting habitat and habitat of principal prey, especially Richardson's ground squirrels (Schmutz et al. 1980; Houston and Bechard 1984; Schmutz 1989). Because ferruginous hawks avoid nesting where over 50% of the land is cultivated (Schmutz 1984), most of the prairie pothole region is presently unsuited to the species.

The ferruginous hawk is presently absent from about 40% of its former breeding range in Alberta (Schmutz 1984) and Saskatchewan (Houston and Bechard 1984). However, Schmutz (1989) reported a 60% increase in the nesting population of ferruginous hawks in study areas in southeastern Alberta from 1982 to 1987 after an increase in abundance of Richardson's ground squirrels. Bechard (1981) thought no breeding ferruginous hawks were left in Manitoba, but Ratcliff and Murray (1984) and Ratcliff (1987) discovered four occupied nests in southwestern Manitoba during 1984–85, the first records since 1927 (Ratcliff and Murray 1984). The number of nesting pairs in Manitoba increased to at least 35 pairs by 1989 (De Smet and Conrad, Manitoba Department of Natural Resources, unpublished report). The ferruginous hawk is still common in portions of the Missouri Coteau of North Dakota and South Dakota (Stewart 1975; Lokemoen and Duebbert 1976; Gilmer and Stewart 1983; South Dakota Ornithologists' Union 1991).

Population structure. The ferruginous hawk is a strongly territorial species that tends to space its nests widely (Lokemoen and Duebbert 1976). Densities of ferruginous hawk nests were estimated in several locations in the prairie pothole region. Schmutz et al. (1980) found 0.12 occupied nests/km^2 in a 335–480-km^2 area of grassland of southeastern Alberta during 1975–77, but Schmutz (1984) estimated a density of 0.02 occupied nests/km^2 in the entire breeding range in southeastern Alberta. Lokemoen and Duebbert (1976) found an average density of 0.06 occupied nests/km^2 in a 269-km^2 area of north-central South Dakota during 1973–74. Gilmer and Stewart (1983) also found an average density of 0.06 occupied nests/km^2 in a 1,259-km^2 area in south-central North Dakota during 1977–79.

Distribution and abundance. Ferruginous hawks were seen in 16 study areas but were a minor (<5%) portion of the sightings of large hawks in all areas except 5 (Fredonia, Hosmer, Morgan, Plaza, Streeter) in the United States (Appendix Table 14; rounding caused the apparent discrepancy in the Kulm study area). Populations were low in nearly all study areas (Fig. 20). In Canada, ferruginous hawks were scarce in eight study areas (50%) and undetected in eight. The ratings include one area (Holden) in 1983 where searches for nests were incomplete because no ferruginous hawks were seen in that area (we assumed if no individuals were seen that no occupied nests were present). Although no occupied nests were found in any study area in Canada, one was found 0.5 km east of one of them (Shamrock) in 1983. In the nine study areas in the United States from which data on nest density were available, ferruginous hawks were common in two (22%), scarce in two (22%), and undetected in five (56%). Occupied nests were found only in two study areas (Fredonia, Kulm); the maximum number during one study area-year was three in one area (0.13/km^2; Appendix Table 15). The species composition data from the eight Central Flyway study areas for which no data on nests were available indicated populations there were similar to populations in other study areas in the prairie pothole region in the United States.

Ferruginous hawks were 0–35% of the sightings of large hawks in individual study area-years (Appendix Table 14) but were the most commonly observed large hawks only in one study area (Hosmer). The two study areas with occupied nests of ferruginous hawks and all six study areas in which sightings of ferruginous hawks were ≥5% of sightings of large hawks were in the prairie along the southwest edge of the region where grassland was most abundant.

Great Horned Owl

Habitat and history. The breeding range of the great horned owl includes nearly all of North America (Robbins et al. 1983), and the species is a common resident throughout the prairie pothole region (Houston 1949; Stewart 1975; Salt and Salt 1976; South Dakota Ornithologists' Union 1991). Unlike the other studied raptors, this species is nonmigratory unless severe environmental conditions force it to leave (Craighead and Craighead 1969). The great horned owl was present throughout the prairie pothole region before settlement (Callin 1980) and has remained fairly common in many areas (Mitchell 1924; N. Criddle 1929; Farley 1932). It is

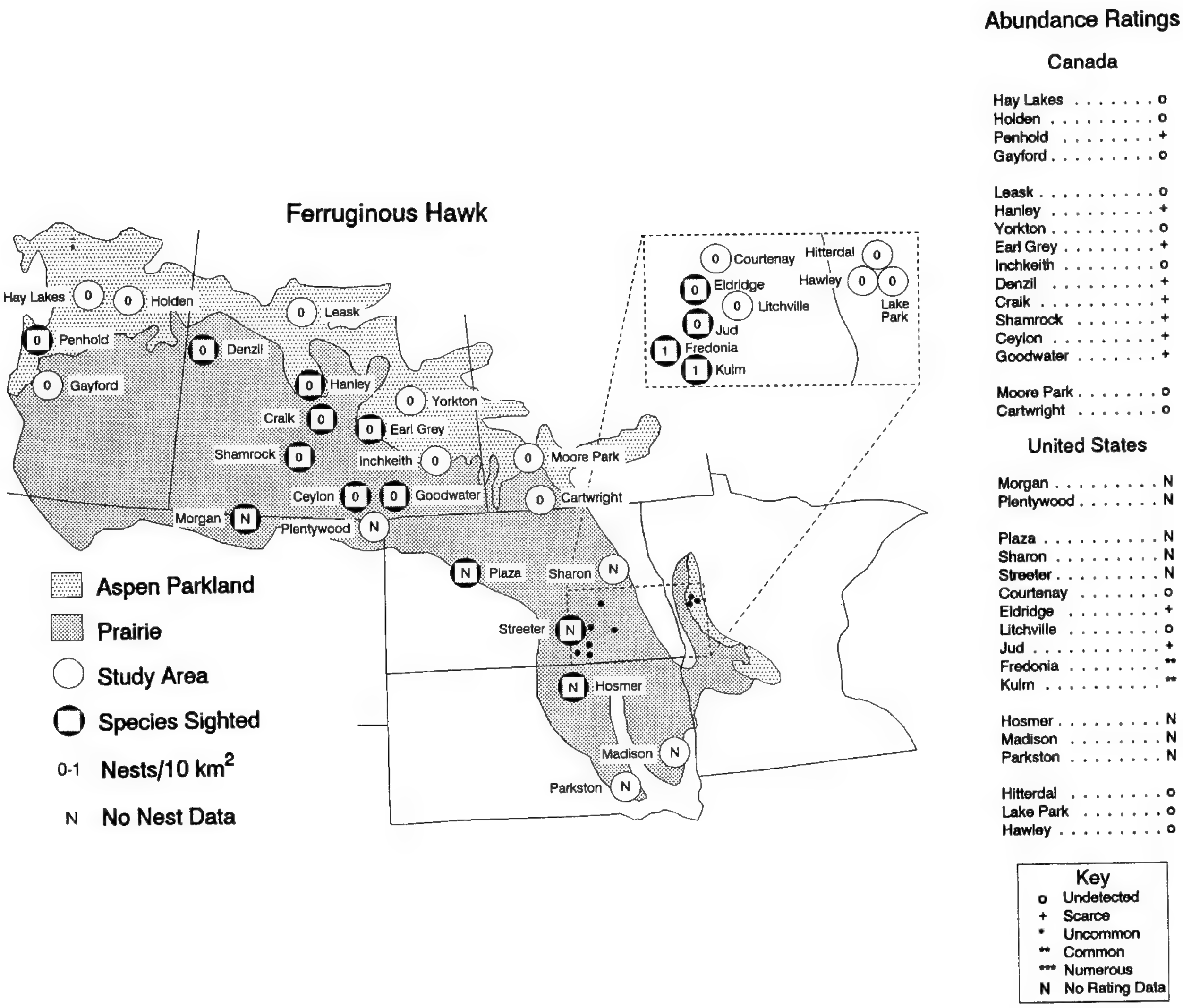


Fig. 20. Density of occupied ferruginous hawk nests (nests/10 km^2) in study areas in the prairie pothole region, and ratings of abundance of ferruginous hawks in each area. Results from each area are for ≥1 year, 1983-88 (Appendix Table 15); results from areas studied in >1 year were averaged.

primarily a woodland species (Bent 1961) and has benefitted greatly from agricultural development. Planting of trees and expansion of the aspen parkland provided great horned owls with nesting and roosting sites in many prairie areas where wooded habitat was previously lacking.

Population structure. The great horned owl is the earliest breeding large raptor and is strongly territorial (Craighead and Craighead 1969). Not all pairs nest, however, and the percentage that nest varies greatly by availability of food (Adamcik et al. 1978; Houston 1987). Thus, the number of occupied nests is not a reliable indicator of the abundance of great horned owls.

Densities of great horned owls of up to 0.77 pairs/km^2 have been reported in Kansas (Baumgartner 1939), but densities in most areas are less than 0.15 pairs/km^2 (Murphy et al. 1969; Adamcik et al. 1978; Petersen 1979). Adamcik et al. (1978) reported an average density of 0.04 pairs/km^2 in aspen parkland in the northwest fringe of the prairie pothole region of Alberta during

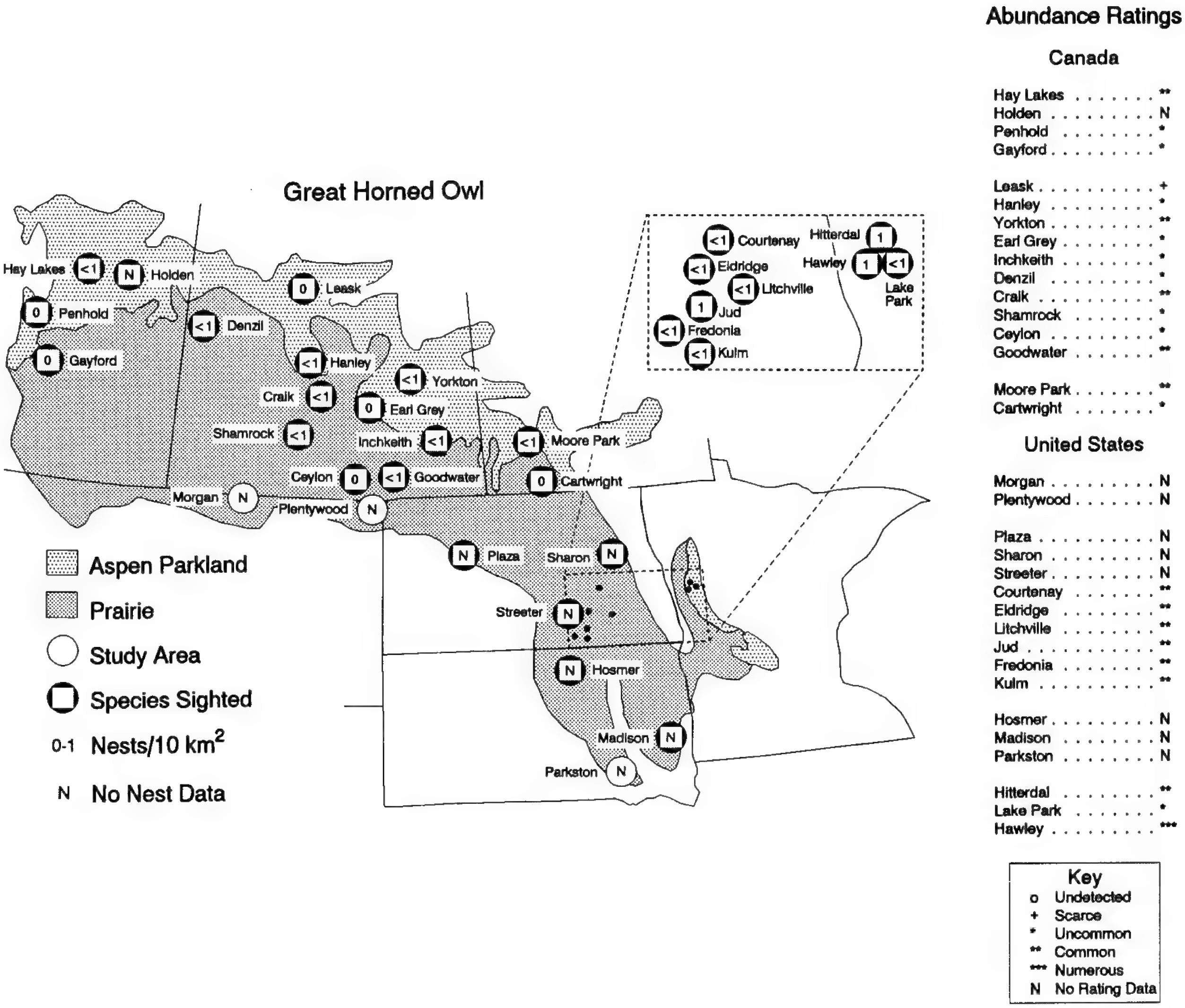


Fig. 21. Study areas in the prairie pothole region in which great horned owls were seen (Appendix Table 13), average density of occupied nests (nests/10 km^2) found in each area (Appendix Table 15), and ratings of abundance of great horned owls in each area. Results from each area are for ≥1 year, 1983–88; results from areas studied in >1 year were averaged.

1966–75. However, densities varied annually from 0.00 to 0.10 pairs/km^2. Bird (1929) and Houston (1960) estimated densities of about 0.19–0.39 occupied nests/km^2 for sites in southern Manitoba and central Saskatchewan. Gilmer et al. (1983) reported an average density of 0.01 occupied nests/km^2 in prairie habitat in south-central North Dakota during 1977–79.

Distribution and abundance. Great horned owls were seen each year in all except three (Morgan, Plentywood, Parkston) study areas (Appendix Table 13) where their presence may have been undetected because no searches for raptor nests were conducted and the number of observer-hours was low. The percentage of study areas with common or more abundant great horned owls was greater in the United States than in Canada (Appendix Table 6). However, that difference may have been influenced by the dates of nest searches, which were about 1 month later in Canada and after some young probably had left nests. In Canada, great horned owls were common in five study areas (31%),

uncommon in nine (56%), and scarce in one (6%; Fig. 21); density was undetermined in one (6%) study area (Holden) where the species was at least common because two nests were found (Appendix Table 15). In the nine study areas where data on nest density were collected in the United States, great horned owls were numerous in one (11%), common in seven (78%), and uncommon in one (11%). Populations in the Central Flyway study areas presumably were similar to populations elsewhere in the prairie. The percentage of study areas with common or more abundant great horned owls did not differ between the prairie and the aspen parkland (Appendix Table 7). Nests of great horned owls were found in 18 of 25 study areas and in 25 of 39 study area-years in which systematic searches for nests were conducted (Appendix Table 15). Except in one study area (Hawley) where four occupied nests were found in 1988, no more than two occupied nests were found in any area in 1 year.

Gulls

Ring-billed and California Gulls

Habitat and history. Ring-billed and California gulls were common and scattered throughout the prairie pothole region before settlement, but populations seemingly declined greatly after settlement when many nesting colonies were eliminated by humans (Stewart 1975; Salt and Salt 1976). Gull eggs were harvested by humans and even served as food in hotels (Houston and Bechard 1982). Nevertheless, large gulls remained common in many areas (Judd 1917; Mitchell 1924; Taverner 1926; Farley 1932; Todd 1947; Bent 1963). During the last several decades, nesting colonies of ring-billed and California gulls became established in many locations in the region and populations of both species are increasing (Stewart 1975). Nesting colonies, mostly of ring-billed and California gulls, are presently scattered throughout most of the region (Stewart 1975; Salt and Salt 1976; South Dakota Ornithologists' Union 1991). Ring-billed gulls are more abundant than California gulls, especially in eastern parts of the region (Houston 1949; Vermeer 1970; Stewart 1975; Callin 1980; South Dakota Ornithologists' Union 1991).

Population structure. Ring-billed and California gulls are colonial nesters and sometimes travel 30 km or more from nesting colonies to feed (Stewart 1975). Colonies in areas with both species are usually a mixture of the two species although interspecific nest segregation is considerable (Vermeer 1970; Stewart 1975). Stewart (1975) identified 11 nesting colonies in the prairie pothole region of North Dakota in 1950–72; populations of 5 were mixed and populations of 6 were only ring-billed gulls. Vermeer (1970) identified 22 nesting colonies (nearly all had both species) in the prairie pothole region of Alberta in 1967. Nesting colonies of both species are also in Saskatchewan and Manitoba (Godfrey 1986). Nesting colonies often contain several hundred to several thousand nests (Anderson 1965; Vermeer 1970).

Distribution and abundance. We did not include ring-billed or California gulls in our surveys, but both species were numerous in two study areas (Gayford, Hay Lakes) and were regularly seen in two others (Leask, Shamrock). A large colony was on four small islands in a lake 2 km north of one of the former (Gayford; 3 km southwest of town of Irricana). A search of two islands on 28 May 1985 revealed 2,944 nests of California gulls but none of ring-billed gulls. More nests seemed to be on the other two islands; the estimated population on one island was two-thirds California gulls and one-third ring-billed gulls. One study area (Hay Lakes) is about 5 km south of Miquelon Lake where several hundred ring-billed and California gulls nested each year 1964–67 (Vermeer 1970). In one study area (Leask), large gulls came from undetermined locations to feed in a landfill. Large gulls in another study area (Shamrock) probably came from Lake Chaplin and Old Wives Lake, 20–30 km away. Large gulls were not abundant in other study areas in Canada.

No data were obtained about the abundance of large gulls in the Central Flyway study areas, but large gulls were occasionally seen in several small unit management study areas.

Annual Variation in Size of Predator Populations

Populations of predator species are subject to annual changes in abundance. The magnitude of such changes was important to interpretation of

our findings because we studied populations in each area 1–3 years.

Annual variation in size of predator populations is caused by mortality, natality, emigration, and immigration. For the species we studied (except northern harrier), mortality rate was the factor most likely to cause major changes in annual abundance. For example, an epizootic or severe human-inflicted mortality could decimate a population in 1 year. In contrast, more gradual changes are expected from (1) the relatively low recruitment rates of most predator species; (2) the tendency of adult predators, especially females, to remain in or return to the same area during successive years; and (3) the tendency of juveniles to disperse. Local populations of northern harriers may fluctuate greatly from year to year from emigration or immigration in response to availability of prey, especially meadow voles (Clark 1972; Hamerstrom 1979).

During our study, we were unaware of major programs to reduce abundance of predators in our study areas other than the removal we conducted in three of the small unit management study areas. However, coyotes may have been removed from or near some study areas, especially in Montana and western North Dakota, to protect livestock. There was evidence of limited killing of certain predators by local residents in a few study areas. For example, several recently killed adult striped skunks were found in one study area (Shamrock) in 1985, one dead adult and two kit raccoons were found (seemingly killed by humans) in another study area (Ceylon) in 1983, and a freshly shot American crow was found in a third study area (Hanley) in 1985. Although most of the studied avian species were protected by law, remains of two red-tailed hawks (in Penhold) in 1985 and a dead northern harrier (in Litchville) in 1988 were found; all were probably killed by humans. Fur prices were high throughout the study (most studied carnivores were economically important furbearers), but harvests in all areas were regulated by provincial, state, and federal agencies.

We were unaware of epizootics among predators or major environmental calamities that could have had a major effect on the abundance of predators in our study areas. However, most data were collected during a drought, which probably contributed greatly to the scarcity of minks and may have affected the abundance of some other species (e.g., northern harrier). The abundance of snowshoe hares (*Lepus americanus*) was declining during our study and probably reduced nesting by great horned owls in the aspen parkland (Rusch et al. 1972; Houston 1987).

A maximum of 18 (number varied by survey type) between-year comparisons of indices was available for predator populations in 16 study areas (10 in Canada and 6 in the United States; Appendix Table 1). In general, the index values for individual species in individual areas changed little between years. For example, the average between-year change (increase or decrease) in the percentage of searched quarter sections with tracks of a particular carnivore species in a study area was 9.2% (SD = 9.74; calculated from data in Appendix Table 5). (The total between-year comparisons for all carnivore species combined was 108, excluding the gray wolf because of its rareness and weasels for which no track searches were conducted.) The average between-year change in the percentage of quarter sections in which black-billed magpies were detected in a study area (12 comparisons) was 1.2% (SD = 2.51) and in which American crows (12 comparisons) were detected, 4.6% (SD = 2.98; calculated from data in Appendix Table 4). The average between-year change in density of American crow nests in a study area (13 comparisons) was 0.14 (SD = 0.15) nests/km^2 (calculated from data in Appendix Table 12). The average between-year change in number of occupied nests by a single species of large hawks (except the northern harrier, for which all nest searches were incomplete, and the ferruginous hawk, which was excluded because of its general scarcity) and the great horned owl combined in a study area was 0.03 (SD = 0.05) nests/km^2 (calculated from data in Appendix Table 15). Although we were unable to establish meaningful criteria for a major change in each species' abundance or to determine the extent of measurement error, we interpret these and similar findings from other surveys as indicative of little change in species abundance and little measurement error. We believe that for most species our findings reflected abundance during several years.

Some major between-year changes in indices of species abundance occurred in a few study areas. In one (Moore Park), the coyote track index increased from 22 to 72% of searched quarter sections from 1983 to 1984 (Appendix Table 5). An

occupied coyote den was in a central portion of that area in 1984 where no evidence of a coyote den and few quarter sections with coyote tracks were found in 1983. Red fox tracks were in several quarter sections in the vicinity of that den in 1983, but none were found in those quarter sections in 1984. The percentage of searched quarter sections with red fox tracks decreased from 60% in 1983 to 44% in 1984. In one study area (Craik), no evidence of red foxes was found in the 8 western-most quarter sections in 1984, but red fox tracks were found in all but one of those quarter sections in 1985. This change accounted for most of the increase from 64% of searched quarter sections with tracks in 1984 to 92% with tracks in 1985 (Appendix Table 5) and indicated that a new red fox family had become established in the western portion of the study area. Coyote tracks were found in only two of the 8 western-most quarter sections each year.

The decline in one study area (Moore Park) from 70% of quarter sections with raccoon tracks in 1983 to 18% with tracks in 1984 (Appendix Table 5) seemed to reflect a major population decline. In 1984, raccoon tracks were found at only a few locations throughout that study area despite improved conditions for finding raccoon tracks. The cause of the decline was undetermined.

Measurement error from variable tracking conditions probably had the most influence on track indices for striped skunks, badgers, and minks. The greatest annual change in the track index for the striped skunk (Shamrock from 1984 to 1985; Appendix Table 5) was not supported by a comparable change in capture rates (Appendix Table 9). Although several dead striped skunks were found discarded in a pile there in 1985, more important to interpretation of the track data was the very poor tracking conditions from drought and untimely strong winds.

The indices of the annual observation (Appendix Table 10) and capture rates (Appendix Table 11) of Franklin's ground squirrels provided similar indicators of relative abundance except where (Moore Park) the large decline in the observation rate from 1983 to 1984 was inconsistent with the substantial increase in the capture rate. Measurement error was the suspected cause of the discrepancy. Nevertheless, both indices in both years indicated that Franklin's ground squirrels were much more abundant there than in most other study areas.

Indices of avian species except the black-billed magpie, northern harrier, and great horned owl were the number of occupied nests that were subject to little measurement error. The largest annual variations of avian species occurred where (Penhold) most bird indices declined from 1984 to 1985 (Appendix Tables 4, 12, 13, and 15). No reasons were found for the apparent declines, although human-inflicted mortality of red-tailed hawks was suspected. Northern harriers are noted for large variation in annual abundance (Clark 1972; Hamerstrom 1979, 1986). Where substantial changes in the abundance of northern harriers occurred (Hay Lakes, Fredonia; Appendix Table 15), they were probably in response to changes in availability of meadow voles.

Factors of Abundance and Distribution

Habitat Changes

Habitat provides essential requisites for survival of species. Suitable habitat, however, may be underutilized or even unoccupied by a species for a variety of reasons such as excessive human-inflicted mortality or interspecific relations that result in one species excluding another. Although separation of influences on species abundance is difficult, habitat changes since settlement clearly have had major effects on the distribution and abundance of many predator species in the prairie pothole region.

Major habitat changes affecting predator populations in the region have been (1) conversion of grassland and wetland to annually tilled cropland; (2) expansion of the aspen parkland zone; and (3) establishment of farmsteads with associated windbreaks, food sources (e.g., refuse, grain), water, and human presence. These changes fragmented natural habitats and increased structural diversity of habitats. Changes that harmed nearly all predator species include establishment of large annually tilled fields, destruction of wetlands, and certain farming practices such as fallowing of land and application of chemicals. Changes that fa-

vored many predator species include establishment of tree plantings, farmsteads, certain crops, rock and brush piles, refuse sites, impoundments, and road grades. Both types of changes occur throughout the region.

The magnitude and type of changes determine whether changes of habitat may be beneficial or detrimental to a particular predator species. Changes from small diversified farms with livestock and several crop types probably favor nearly all predator species in all parts of the prairie pothole region. Conversely, large monotypic grain-farming operations are detrimental to nearly all predator species (see Schmutz [1989] regarding certain raptors).

In large parts of the prairie pothole region, the detriments to predator populations from habitat degradation presently outweigh the benefits from increased structural diversity of habitat. Before 1940, farming was highly diversified and farm units were small (Bird 1961; Robinson 1966; Kiel et al. 1972). Small habitat units of diversified farms were attractive to many predator and prey species. After the 1940's, farm units became less diversified and greatly increased in size (Robinson 1966). This was especially true in the prairie of southeastern Alberta, southern Saskatchewan, and eastern North Dakota where entire quarter sections and even sections are tilled annually (Fig. 4). Nevertheless, these areas still support diverse predator communities.

Mammalian predator species that clearly benefitted from habitat changes in the prairie pothole region are the coyote, red fox, raccoon, and Franklin's ground squirrel. More diverse and more stable food supplies became available to the coyote and red fox. However, major changes in abundance of these two canids can probably not be attributed primarily to habitat changes. Human-inflicted mortality and interspecific relations of canids seem to have been dominant factors of the changes in distribution and relative abundance of canid species (Sargeant 1982). For the raccoon, habitat changes provided food and shelter that previously were sufficient to maintain populations only in wooded riverine habitat in southeastern portions of the region (Bailey 1926; Cowan 1974). Habitat changes allowed raccoons to greatly expand their distribution and abundance in the region, but other factors such as incompatibility with other species (possibly coyotes) and human-inflicted mortality probably inhibited the response of raccoons to habitat changes. For the Franklin's ground squirrel, increased habitat diversity and expansion of the aspen parkland zone probably elicited an expansion of range into the prairie.

The abundance of minks in the prairie pothole region has probably not changed greatly since presettlement times. Although minks depend on wetlands (Eagle and Whitman 1987), drainage in most of the region has probably not been sufficient to cause major population changes except where wetland losses were extensive. In some areas, especially during drought years, stock dams, dugouts, impoundments, and ditches created deeper and more stable water for minks and their prey.

Striped skunks have probably also benefitted from agricultural development. They make extensive use of human habitation (e.g., often rear young and forage at farmsteads [A. B. Sargeant and R. J. Greenwood, unpublished data]). They are omnivorous and forage extensively for insects (Jones et al. 1983). Even intensively farmed areas support at least moderate densities of striped skunks.

In the prairie pothole region, several avian predator species have benefitted from habitat changes, especially expansion of the aspen parkland and the widespread planting of trees for windbreaks. The occurrence of American crows and great horned owls throughout the region and the expansion of the range of the red-tailed hawk are closely linked to the increased area of tall trees and wooded habitat (Houston and Bechard 1983). Black-billed magpies probably also benefitted from the planting of trees and availability of food from agricultural activities.

Harm from habitat change is more subtle than the benefits and relates largely to losses of habitat quality and prey. Of the mammals, the badger and long-tailed weasel were probably most severely affected. Both species feed largely on vertebrates (Jones et al. 1983) in grasslands. Neither species is suited to or allowed to make extensive use of human habitation. Conversion of grassland to cropland, which was almost complete in some of our study areas (Table 1), has greatly reduced the amount of available prey for these species.

Some avian predator species have also been harmed by habitat changes, especially by reductions in amount of grasslands and associated losses

of prey. The abundance and breeding range of the ferruginous hawk have been severely reduced (Evans 1982; Schmutz 1984). Abundance of the northern harrier also declined, probably at least partially from losses of grassland and wetland habitats (Evans 1982). Abundance of the Swainson's hawk does not seem to have been reduced as much by losses of grassland habitat as by expansion of the aspen parkland.

Direct Human Influences

The effect of deliberate killings of predators in the prairie pothole region by humans was substantial during certain periods, especially from the onset of settlement to the mid 1930's. During the latter half of that period, the region was occupied by many more rural residents than now (Strange 1954; Robinson 1966). Those rural residents were knowledgeable of the land and its resources, and many of them used fur as a source of income (Hamilton and Fox 1987). Moreover, many rural people had an ingrained dislike of predators. Although records of the abundance of predators during this period are scant, many species were clearly under severe attack by humans for a variety of reasons (e.g., egg collecting, food gathering, fur harvesting, bounties, predator control), and populations of many species were reduced to or held at low levels. The effect of extensive killing of mammals by humans is exemplified by extirpation (by trapping, shooting, and poisoning) of the gray wolf from nearly all of the region by the early 1900's. Fur harvesting was especially intense during the 1910's and 1920's when pelts were valuable and regulations were limited and weakly enforced (Dearborn 1920; Lawyer and Earnshaw 1921; Sargeant 1982). Populations of nearly all carnivore species probably were greatly reduced, at least locally (Osborn and Anthony 1922; N. Criddle 1929; Bird 1930; Drescher 1974; Sargeant 1982). Even though habitat was favorable, intensive harvesting of species that were not common when settlement began (e.g., red fox, raccoon) coupled with human-inflicted mortality for other reasons and interspecific competition probably prevented population expansion for several decades. Because of their size and relatively small home ranges, weasels were perhaps less affected than most other predator species by human-inflicted mortality but were also extensively trapped (Fagerstone 1987).

During the 1940–60's, when fur prices were generally low, animal damage (livestock and wildlife) and control-of-diseases programs that included widespread use of toxicants and bounties resulted in deaths of tens of thousands of carnivores annually in various provinces and states of the prairie pothole region. For example, 10,000–35,000 red foxes were submitted for bounty annually in North Dakota during 1945–58 (Adams 1961), and about 250,000 coyotes were killed in the agricultural region of Alberta during 1951–56 (Ballantyne 1958). These programs failed to reduce red fox populations to low levels but probably had considerable effect on abundance of coyotes in many intensively cultivated areas (Adams 1961).

Population changes of avian predators were similar to that of mammals but for different reasons. Initially, egg collectors helped reduce certain raptor populations (Houston and Bechard 1982). Later, raptors (collectively called chicken hawks) were regarded as harmful because of their actual or presumed threats to poultry and small game (Mitchell 1924; Fox 1939; Newton 1979) and were indiscriminately killed (N. Criddle 1929; Fox 1939; Salt 1939; Williams 1946; Kirkpatrick and Elder 1951; Evans 1982; Houston and Bechard 1984). This indiscriminate killing continued largely unabated into the 1950's and seemingly persists in some localities at greatly reduced levels (Houston and Bechard 1984).

American crows and black-billed magpies were severely persecuted during the 1920–50's to reduce predation on game birds, including waterfowl (Sowls 1955; Johnson 1964). People in many areas were encouraged by bounties and other rewards to destroy the birds and their nests, but the effects of these controls are largely undetermined. After settlement, gull colonies were decimated by egg collectors and by other factors (Stewart 1975; Salt and Salt 1976).

Inter- and Intraspecific Interactions

Relations between predator species range from antagonistic to beneficial. Of particular consequence to duck production in the prairie pothole region is that gray wolves suppress the abundance

of coyotes (Mech 1970; Berg and Chesness 1978; Fuller and Keith 1981; Carbyn 1982) and coyotes suppress the abundance of red foxes (N. Criddle 1929; Sargeant 1982; Voigt and Earle 1983; Sargeant et al. 1987a; Harrison et al. 1989). The primary mechanism for suppression seems to be interference competition (Voigt and Earle 1983). Hence, extirpation of the gray wolf from the region by the early 1900's was a major causative factor of subsequent changes in the distribution and abundance of other canid species in the region.

Effects of interspecific interactions among other predator species are largely undetermined but may also be considerable. For example, red foxes and presumably coyotes and hawks prey on Franklin's ground squirrels (Choromanski-Norris et al. 1989), and red foxes prey on weasels (Latham 1952). Red foxes, striped skunks, and minks use burrows dug by other species. Raccoons, which are excellent tree climbers, prey on eggs and nestlings of American crows (Chamberlain-Auger et al. 1990) and black-billed magpies (Jones 1958). Conversely, great horned owls use platforms of other raptors for nesting (Dunstan and Harrell 1973; McInvaille and Keith 1974; Houston 1975; Bohm 1980). The antagonism between great horned owls and American crows is well-known (Houston 1960; Craighead and Craighead 1969), and great horned owls occasionally prey on certain other owls and hawks (Errington et al. 1940; Craighead and Craighead 1969; Dunkle 1977) and on striped skunks (Seton 1953). These are complex relations about which little is known. Understanding interspecific relations may help explain changes in the composition of predator populations in the prairie pothole region and may have predictive value.

Mammals

Data from our track surveys allowed us to examine relations among the abundance of several carnivore species (Table 2). Canids had the most complete occupancy of study areas of all studied species and species-groups. All study areas and probably all quarter sections of each area were occupied by either coyotes, red foxes, or both during all study area-years. Tracks of one or both species were found in 93% of all twice-searched quarter sections and in 62% of those searched once. The coverage of study areas by these species conformed to that expected from the spatial arrangement of sympatric coyotes and red foxes in North Dakota described by Sargeant et al. (1987a) and included: (1) an entire study area with tracks of one species; (2) a contiguous block of quarter sections, sometimes almost entire study area, with tracks of both species (areas of interspecific territory overlap); and (3) contiguous quarter sections with tracks of one species separated by quarter sections with tracks of both species (study area that crossed interspecific territory boundaries; Fig. 22). When the percentage of quarter sections of study areas with coyote tracks increased, the percentage with fox tracks decreased (Table 2), which supports findings of others that red foxes tend to avoid living in coyote territories (Voigt and Earle 1983; Sargeant et al. 1987a; Harrison et al. 1989).

Circumstantial evidence suggests that coyotes may suppress raccoon populations in the prairie pothole region (Cowan 1973; Stelfox 1980), and Clark et al. (1989) found that coyotes occasionally kill raccoons. In our study areas, indices from tracks revealed a decreased abundance of raccoons with an increased abundance of coyotes (weak correlation; Table 2), giving some credence to the hypothesis that coyotes suppress abundance of raccoons. However, coyotes were numerous in a study area (Yorkton) with the highest raccoon index in

Table 2. *Correlations between occurrence of tracks (% of searched quarter sections with tracks[a]) of pairs of mammalian carnivore species in study areas in the prairie pothole region, 1983–88.*[b]

Species pairs[c]	r	P
Coyote–red fox	−0.86	<0.001
Coyote–raccoon	−0.64	<0.001
Coyote–striped skunk	<0.01	0.988
Coyote–badger	0.24	0.258
Red fox–raccoon	0.63	<0.001
Red fox–striped skunk	0.14	0.504
Red fox–badger	−0.11	0.619
Raccoon–striped skunk	−0.10	0.639
Raccoon–badger	<0.01	0.992
Striped skunk–badger	−0.38	0.060

[a] Includes only study area-years where two searches for tracks were made.
[b] The mink was excluded because of its low occurrence or absence in most study areas.
[c] Number of study area-years equals 25 for all species.

Canada (Figs. 5 and 8). Possibly, the greater abundance of abandoned farm buildings in that study area offered denning and resting raccoons additional protection from coyotes.

Coyotes (Godin 1982) and badgers (Gilbert 1960; Sargeant et al. 1982) occasionally prey on striped skunks, and there is evidence of mutual (Lehner 1981) albeit sometimes fatal attraction (Rathbun et al. 1980) between coyotes and badgers. However, we found no relation between track indices of coyotes and striped skunks, badgers and striped skunks, and coyotes and badgers (Table 2). No evidence suggested that interactions between other pairs of sympatric mammalian predator species affected their abundance. The concomitant increases of track indices of red foxes and raccoons (Table 2) were probably a reflection of the increasing abundance of these species with a decline in populations of coyotes. We found no literature to suggest red foxes and raccoons mutually benefit one another.

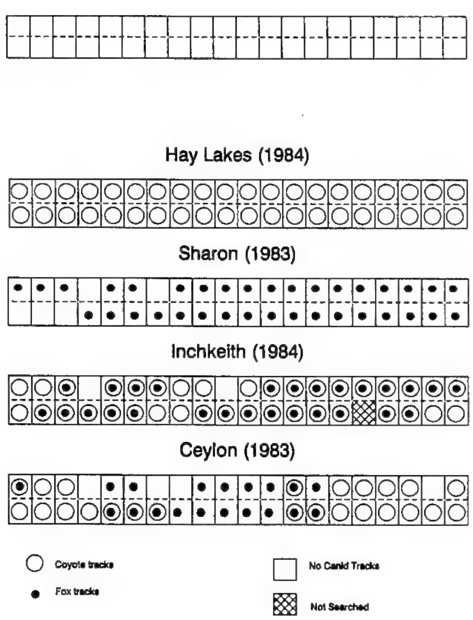


Fig. 22. Examples of spatial arrangements of coyotes and red foxes in four selected study areas in the prairie pothole region as revealed by presence or absence of tracks found in quarter sections during two systematic searches for tracks in April–June (only one search was conducted in the Sharon study area), 1983–84.

Birds

Published evidence of interspecific segregation of nests of studied raptors was greatest by sympatric great horned owls and red-tailed hawks (McInvaille and Keith 1974; Schmutz et al. 1980), even though red-tailed hawks frequently nest near great horned owls (Orians and Kuhlman 1956; Hagar 1957; Dunstan and Harrell 1973; Houston 1975). Schmutz et al. (1980) observed aggression by Swainson's hawks toward both ferruginous hawks and red-tailed hawks. They also found that ferruginous hawks that nested within 0.3 km and Swainson's hawks that nested within 0.2 km of nests of another buteo species were less successful in fledging young than conspecifics that nested farther from nests of another buteo species. Rothfels and Lein (1983) reported interspecific territoriality among sympatric Swainson's hawks and red-tailed hawks.

Our tests of interspecific relations between all two-way combinations of the three raptor species (Swainson's hawk, red-tailed hawk, and great horned owl) revealed only the red-tailed hawk and great horned owl tended to nest near each other and no species tended to avoid nesting near another (Table 3). The observed number was three times greater than the expected number of nests of red-tailed hawk within 0.5 km of an occupied nest of a great horned owl. This tendency was not uniformly strong in all study area-years and was most pronounced (Holden) in 1983 and (Hawley, Hitterdal, Litchville) in 1988.

We do not believe interspecific attraction occurs between red-tailed hawks and great horned owls. Conversely, these species exhibit mutual antagonism; great horned owls occasionally prey on nestling red-tailed hawks (Craighead and Craighead 1969; Luttich et al. 1971; McInvaille and Keith 1974) and red-tailed hawks occasionally attack great horned owls (Smith 1970; Palmer 1988a). Red-tailed hawks clearly have strong philopatry and build sturdy nest platforms to which they often add nest material in successive years (Luttich et al. 1971). Great horned owls use nests of other species, especially of red-tailed hawks (Orians and Kuhlman 1956; Dunstan and Harrell 1973; Houston 1975; Petersen 1979). Because they seldom migrate and nest much earlier than the migratory red-tailed hawks (Bent 1961; Stewart 1975), great

horned owls often usurp seasonally vacated nests of red-tailed hawks. A returning red-tailed hawk pair, finding its nest occupied, probably builds a new nest nearby. The lack of a significant tendency by great horned owls and Swainson's hawks to nest near one another (Table 3) may be because Swainson's hawks nest later and closer to the ground (Schmutz et al. 1980; Palmer 1988b), build less sturdy nests (A. B. Sargeant and M. A. Sovada, personal observation), and are more vulnerable to aggression by great horned owls than red-tailed hawks (Dunkle 1977).

Our examinations of interspecific interactions revealed that across all study area-years American crows tended to avoid nesting within 0.5 km of red-tailed hawks (Table 3). Although no such relation was detected between American crows and Swainson's hawks, the test for homogeneity of the association revealed a tendency by American crows to aggregate nests around nests of Swainson's hawks in some study area-years but to avoid or have no nest site association with nests of Swainson's hawks in other study area-years (Table 3).

Our examinations of intraspecific interactions were restricted to examinations of spacing of nests by several avian predator species. Previous investigations revealed American crows may cluster or space nests (Good 1952; Bent 1964), but that the raptor species we studied, except the northern harrier, are territorial and tend to space their nests widely (Bent 1961; Craighead and Craighead 1969; Schmutz et al. 1980; Rothfels and Lein 1983; Hamerstrom et al. 1985). In our study, American crows tended to aggregate their nests, whereas red-tailed hawks avoided nesting near each other (Table 3). The tendency by American crows to aggregate their nests was not consistent across all study area-years but was particularly strong in two (Moore Park and Inchkeith) in 1984 and in four (Shamrock, Inchkeith, Earl Grey, Yorkton) in 1985. Red-tailed hawks consistently avoided nesting near each other in all study area-years. Swainson's hawks did not demonstrate intraspecific relations in nest spacing (Table 3) in contrast to findings of Rothfels and Lein (1983). Data on great horned owls were too limited to permit meaningful analysis.

Table 3. *P-values and odds ratios from Mantel-Haenzel tests (Fleiss 1973) of inter- and intraspecific relations of nest spacing by avian predator species in study areas in the prairie pothole region, 1983–88.*[a,b]

Species pair or species	N[c]	Odds[d]	*P*-value: Association[e]	*P*-value: Homogeneity[f]
Interspecific				
American crow–great horned owl	17	0.41	0.193	0.950
Red-tailed hawk–great horned owl	12	3.38	0.002	<0.001
Swainson's hawk–great horned owl	18	0	0.252	>0.999
American crow–red-tailed hawk	19	0.35	0.005	0.992
Swainson's hawk–red-tailed hawk	11	0.75	0.763	0.988
American crow–Swainson's hawk	20	1.35	0.260	<0.001
Intraspecific				
American crow	25	2.02	<0.001	<0.001
Swainson's hawk	19	0.46	0.299	>0.999
Red-tailed hawk	18	0.12	0.002	>0.999

[a] Association refers to an overall tendency to avoid or aggregate.
[b] Homogeneity indicates the consistency of the association across study area-years.
[c] Number of study area-years.
[d] Odds <1 indicates avoidance of nesting near each other; odds >1 indicates aggregation of nests.
[e] P-value based on chi-squared distribution with 1 degree of freedom.
[f] *P*-value based on chi-squared distribution with N−1 degrees of freedom.

Population Trends

Our review of the literature revealed that throughout the prairie pothole region population levels of nearly all predator species have varied greatly since settlement began. Populations of species that were unable to adapt to the rapidly changing environment or were wantonly over-harvested for profit or because they conflicted with human interests diminished rapidly in abundance, distribution, or both, some to extirpation. Populations of other species increased by taking advantage of newly created habitats, absences of certain competitors, or both. The magnitude of changes that occurred during the late 1800's was enormous.

Changes during the early 1900's to the mid-1930's in levels of predator populations were more gradual, but exploitation of nearly all predator species affecting ducks was extremely heavy (Johnson 1964). Numerous authors refer to heavy exploitation and low numbers of most predator species during this period (Dearborn 1920; Osborn and Anthony 1922; Bird 1930; Farley 1932; Kiel et al. 1972; Sargeant 1982). A notable exception was that abundance of American crows expanded greatly in spite of severe persecution (Johnson 1964). Ducks nesting in the prairie pothole region during this period were probably at lower risk from predation than during any other period since settlement began.

The severe drought and the economic depression of the mid-1930's caused abandonment of large numbers of farmsteads (Robinson 1966). Declining fur prices reduced human harvests of many predators. In the early 1940's, World War II further reduced direct human influence on the abundance of predators, even though fur prices surged for a few years, through military conscriptions and restrictions on ammunition and motorized transportation (Bihrle 1990). Modern game management began early in this period and collection of quantitative data about the abundance of predators commenced (Adams 1961). Populations of at least three major predator species affecting duck production (red fox, raccoon, and American Crow) expanded rapidly in various parts of the region (Adams 1961; Kiel et al. 1972; Sargeant 1982; Sanderson 1987).

Post World War II brought about mechanized agricultural activities and a mobile public with strong interests in outdoor activities but low regard for most predators (Kirkpatrick and Elder 1951; Sargeant 1982). Pelt prices of many predator species, especially those with long fur, were exceptionally low from the mid-1940's until the late 1960's, especially in the United States. Red fox and raccoon populations continued to expand in the United States portion of the region and bounties were widely used in attempts to reduce numbers of red foxes and other predators (Hubert 1982). However, bounties generally failed to reduce populations to low levels. Populations of most avian predators, especially raptors, did not flourish and some declined because of increased use of agricultural chemicals (e.g., DDT, which caused eggshell thinning among some raptors [Anderson and Hickey 1972; Evans 1982]), continued deliberate killing by humans, and continued habitat losses.

A particularly important activity during the 1940–60's was the effective widespread use of toxicants, especially compound 1080 (sodium monofluoroacetate) for the control of coyotes. Compound 1080 was widely used beginning in the late 1940's in the United States and later in Canada (U.S. Fish and Wildlife Service 1978; Andelt 1987). Bounty records showed that red foxes did not become common in western North Dakota until the mid-1950's, after coyote populations had been reduced (Adams 1961). Stoudt (1971) reported that red foxes became numerous and raccoons first appeared in the Redvers area of southeastern Saskatchewan shortly after coyote numbers were greatly reduced by a control program in the early 1950's that involved use of compound 1080. By the late 1960's, red foxes were abundant throughout nearly all of the southeastern portion of the prairie pothole region. Attitudes toward predators then began to change as a result of growing concern for predators, especially raptors, and the high costs and general ineffectiveness of bounties. By the late 1960's, bounties on predators had been largely discontinued (Hubert 1982; Slough et al. 1987).

Since the late 1960's, growing concern for the welfare of wildlife, including predators (Cain et al. 1972), resulted in restrictions in predator control programs (U.S. Fish and Wildlife Service 1978) and increased attention to management of furbearers and protection of avian predator species. Use of toxicants was greatly reduced throughout the prairie pothole region early in this period (U.S. Fish and Wildlife Service 1978). Also, the use of

aircraft, snowmobiles, and other all-terrain vehicles for pursuing coyotes and red foxes was greatly restricted in nearly all areas. For example, in 1968 the red fox in North Dakota was unprotected and could be legally killed anytime by almost any means including aerial hunting, destruction of pups in dens, and toxicants. By 1974, the red fox had been reclassified as a furbearer with a 197-day harvest season. Destruction of pups in dens, aerial hunts, chases with snowmobiles, and toxicants were banned except under special circumstances. During this period, raptors were afforded considerable protection in Canada and the United States (Bond 1974; Heintzelman 1979). In the United States, the American crow was protected as a migratory bird and could be killed only during established seasons. When our study commenced, only a few predator species were still unprotected in most areas (e.g., striped skunk, Franklin's ground squirrel, and, only in Canada, American crow and black-billed magpie).

Whereas the complete protection of raptors resulted from public concern for such birds, much of the concern for carnivores after the 1960's resulted from resurgence of high fur prices that rivaled those of the early 1900's. However, because of government regulations, fur harvests reduced few mammalian predator populations throughout large areas to low levels during this period. In southeastern portions of the prairie pothole region, the coyote benefitted from harvest restrictions and expanded its populations (A. B. Sargeant, personal observations). The reverse may have occurred in some heavily farmed areas of Canada where coyotes had been present but were heavily harvested.

Nobody can accurately predict the magnitude of changes in the future abundance and distribution of predator species. Gradual changes will probably occur as habitats continue to be altered. Changes in direct and indirect human-inflicted mortality rates of species, especially severe curtailments of human-inflicted mortality, may result in expansion of the population of some species to the detriment of others. Questions to be answered include: Will raptor populations increase substantially and result in interspecific exclusions, will American crows become numerous again in the southern portion of the region, and will coyote populations expand further and cause major declines in abundance of red foxes and possibly raccoons?

Predator Communities

Every quarter section we examined was occupied by several predator species. Although we could not determine the composition and relative abundance of predators in each quarter section, we rated the abundance of nearly all species and species-groups known or believed to be resident in one or more study areas (Figs. 5–21). A species was generally present throughout a study area where it was rated common or numerous. Exceptions included spatial segregation of coyotes and red foxes and occasional instances when a species was abundant in part of a study area but uncommon or absent in the remaining area. The distributions of uncommon or scarce species were often restricted to small portions of study areas (e.g., area around the only American crow nest). Excluding gulls, the number of species per study area averaged 12.2 (SD = 1.60); the number of common or numerous species averaged 6.0 (SD = 1.54; minimal because abundance of weasels in all study areas and abundance of minks and raptors in some study areas were not determined; Table 4 [mammals], Table 5 [birds]).

The species composition and abundance of predator species in study areas varied within and among parts of the prairie pothole region. The striped skunk, American crow, and northern harrier were the only species detected in all study areas (Tables 4 and 5). The red fox was detected in all but one study area but was rated scarce in two (Fig. 7) where tracks were found in <7% of searched quarter sections (Appendix Table 5). All species except the striped skunk and northern harrier were undetected or scarce in at least one study area, and two mammals (gray wolf, mink) and two birds (common raven, ferruginous hawk) were undetected in >50% of study areas (Tables 4 and 5).

Distribution and especially abundance of some predator species was influenced by habitat type. Species of the aspen parkland zone were the Franklin's ground squirrel, black-billed magpie, American crow, and red-tailed hawk (Appendix Table 7). Species of the prairie zone were the badger and Swainson's hawk (Appendix Table 7). The ferruginous hawk also was clearly most closely associated with the prairie (Fig. 20), but populations were too low to demonstrate the relation (Appendix Table 7).

Table 4. *Number and relative abundance of mammalian predator species affecting duck production by study area and province or state in the prairie pothole region.*[a,b]

Area[d]	Year(s)	Number species present	Number species ≥ common[e]	Relative abundance[c] Coyote (1,2,3)	Red fox (1,2,3)	Raccoon (2)	Striped skunk (2)	Badger (2,3)	Mink (1,2,3)	Weasels[f] (1,2,3)	Franklin's ground squirrel (2)
Canada											
Alberta											
Gayford	1985	4	2	4	0	0	2	3	0	d	0
Hay Lakes*	1983–84	5	2	4	1	0	3	0	0	d	1
Holden*	1983	7	2	4	2	1	3	1	0	d	1
Penhold*	1984–85	5	3	4	3	0	3	2	0	d	0
	Average	5.3	2.3								
Manitoba											
Cartwright	1983	6	4	3	3	3	3	2	0	u	2
Moore Park*	1983–84	9[g]	5	3	3	3	3	2	1	d	3
	Average	7.5	4.5								
Saskatchewan											
Ceylon	1983–84	8	5	3	3	3	3	3	1	d	1
Craik	1984–85	7	4	3	4	3	4	1	1	u	1
Denzil	1984–85	5	3	3	4	0	4	1	0	d	0
Earl Grey*	1985	6	4	4	3	2	3	1	0	u	4
Goodwater	1983	6	5	3	3	3	3	3	0	u	2
Hanley*	1983–85	6	3	4	2	2	4	2	0	u	3
Inchkeith*	1984–85	7	5	4	3	3	3	3	0	d	2
Leask*	1984–85	7	4	4	3	1	3	3	0	d	1
Shamrock	1983–85	7	4	4	3	2	3	3	0	d	1
Yorkton*	1985	7	3	4	1	4	3	1	0	d	2
	Average	6.6	4.0								
United States											
Minnesota											
Hawley*	1987–88	7	4	0	4	4	3	1	3	d	1
Hitterdal*	1988	6	4	0	4	4	3	0	3	d	2
Lake Park*	1987–88	6	4	0	4	4	3	1	3	u	1
	Average	6.3	4.0								
Montana											
Morgan	1983	4	4	3	3	0	4	3	u	u	0
Plentywood	1983	5	5	3	3	3	4	4	u	u	0
	Average	4.5	4.5								
North Dakota											
Courtenay	1988	6	3	1	4	3	3	2	2	u	0
Eldridge	1987–88	7	4	3	4	3	3	2	1	u	1
Fredonia	1987–88	8	4	3	3	3	3	2	2	d	1

Table 4. *Continued.*

Area[d]	Year(s)	Number species present	Number species ≥ common[e]	Relative abundance[c] Coyote (1,2,3)	Red fox (1,2,3)	Raccoon (2)	Striped skunk (2)	Badger (2,3)	Mink (1,2,3)	Weasels[f] (1,2,3)	Franklin's ground squirrel (2)
Jud	1987–88	8	5	3	3	4	3	3	2	d	1
Kulm	1988	7	6	3	4	3	3	3	3	u	1
Litchville	1987–88	6	4	0	4	3	3	2	3	u	1
Plaza	1983	6	4	2	4	4	3	3	u	d	0
Sharon	1983	6	4	0	4	3	4	3	u	d	2
Streeter	1983	6	5	3	3	4	3	4	u	u	1
	Average	6.7	4.3								
South Dakota											
Hosmer	1983	6	4	2	3	3	3	3	u	d	0
Madison	1983	6	4	2	3	4	3	3	u	d	0
Parkston	1983	7	5	3	3	4	3	3	u	d	1
	Average	6.3	4.3								
Total areas detected (%)				85	97	85	100	94	36	61	73
Total areas ≥ common (%)				73	85	70	97	48	20[h]	—	9

[a] Includes only predators known or thought to be resident in one or more study areas, 1983–88.

[b] Numerical abundance ratings are 4 = numerous, 3 = common, 2 = uncommon, 1 = scarce, and 0 = undetected; alphabetical designators (d = detected, u = undetected) are used for species in study areas for which data were insufficient to rate relative abundance.

[c] Species denoted with a (1) prey extensively on adult ducks, species denoted with a (2) prey extensively on duck eggs, and species denoted with a (3) are known or thought to prey extensively on ducklings.

[d] Study areas denoted with an asterisk (*) are in the aspen parkland; all other study areas are in the prairie.

[e] Minimal because the mink (some study areas) and weasels were not rated.

[f] Includes ermine and long-tailed weasel.

[g] Includes the gray wolf, which was found only in the Moore Park study area and rated scarce.

[h] Based only on data from study areas where abundances of predators were rated.

Table 5. *Number and relative abundance of avian predators species affecting duck production by study area and province or state in the prairie pothole region.*[a,b]

Area[d]	Year(s)	Number present species	Number ≥ common species[e]	Relative abundance[c]: Black-billed magpie (2)	American crow (2)	Northern harrier (1,3)	Swainson's hawk (1,3)	Red-tailed hawk (1,3)	Ferruginous hawk (3)	Great horned owl (1,3)
Canada										
Alberta										
Gayford	1985	6	3	2	3	2	3	3	0	2
Hay Lakes*	1983-84	6	6	3	3	3	3	4	0	3
Holden*	1983	6	5	3	4	3	d	≥3[f]	0	≥3[f]
Penhold*	1984-85	8[g]	3	4	3	2	2	3	1	2
	Average	6.5	4.3							
Manitoba										
Cartwright	1983	6	2	3	3	2	2	2	0	2
Moore Park*	1983-84	6	4	2	3	3	2	4	0	3
	Average	6.0	3.0							
Saskatchewan										
Ceylon	1983-84	6	2	2	2	4	3	0	1	2
Craik	1984-85	7	2	2	3	2	2	2	1	3
Denzil	1984-85	7	2	2	3	2	3	2	1	2
Earl Grey*	1985	7	2	2	3	2	2	3	1	2
Goodwater	1983	6	4	2	3	4	3	0	1	3
Hanley*	1983-85	7	2	3	4	2	2	2	1	2
Inchkeith*	1984-85	6	4	3	3	2	3	3	0	2
Leask*	1984-85	7[g]	3	2	3	3	2	3	0	1
Shamrock	1983-85	7	3	2	3	3	3	2	1	2
Yorkton*	1985	7[g]	3	2	3	2	2	3	0	3
	Average	6.7	2.7							
United States										
Minnesota										
Hawley*	1987-88	4	2	0	2	2	0	3	0	4
Hitterdal*	1988	5	2	1	2	2	0	3	0	3
Lake Park*	1987-88	5[g]	0	0	2	2	0	2	0	2
	Average	4.7	1.3							
Montana										
Morgan	1983	4	0	0[h]	2	d	d	u	d	u
Plentywood	1983	4	0	2[h]	2	d	d	u	u	u
	Average	4.0	0.0							
North Dakota										
Courtenay	1988	5	2	0	1	2	3	2	0	3
Eldridge	1987-88	6	1	0	2	2	2	2	1	3
Fredonia	1987-88	6	4	0	1	4	3	1	3	3

Table 5. *Continued.*

Area[d]	Year(s)	Number present species	Number ≥ common species[e]	Relative abundance[c]: Black-billed magpie (2)	American crow (2)	Northern harrier (1,3)	Swainson's hawk (1,3)	Red-tailed hawk (1,3)	Ferruginous hawk (3)	Great horned owl (1,3)
Jud	1987–88	6	2	0	2	2	3	2	1	3
Kulm	1988	6	2	0	2	2	2	2	3	3
Litchville	1987–88	5	2	0	1	2	3	2	0	3
Plaza	1983	6	—	0	2	d	d	d	d	d
Sharon	1983	5	—	0	2	d	d	d	u	d
Streeter	1983	5	—	0	2	d	d	u	d	d
	Average	5.6	2.2[h]							
South Dakota										
Hosmer	1983	7	—	1	2	d	d	d	d	d
Madison	1983	5	—	0	2	d	d	d	u	d
Parkston	1983	5	—	0	2	d	d	d	u	d
	Average	5.7	—							
Total areas detected (%)				58	100	100	91	85	48	94
Total areas ≥ common (%)				18	45	32[h]	46[h]	44[h]	8[h]	56[h]

[a] Includes only predators known or thought to be resident in one or more study areas, 1983–88. Excludes ring-billed gulls and California gulls which were not surveyed.

[b] Numerical abundance ratings are 4 = numerous, 3 = common, 2 = uncommon, 1 = scarce, and 0 = undetected; alphabetical designators (d = detected, u = undetected) are used for species in study areas for which data were insufficient to rate relative abundance.

[c] Species denoted with a (1) are known or thought to prey extensively on adult ducks, species denoted with a (2) prey extensively on duck eggs, and species denoted with a (3) are known or thought to prey on ducklings.

[d] Study areas denoted with an asterisk (*) are in the aspen parkland; all other study areas are in the prairie.

[e] Minimal because some species in some study areas were not rated.

[f] Survey data were incomplete but results showed species was at least common.

[g] Includes the common raven in which was found only in Penhold, Leask, Yorkton, and Lake Park study areas and was rated uncommon or scarce in each.

[h] Based on only rated study areas.

Abundance of some predator species was related to country. This relation probably reflected latitude and its influence on climate, habitat, and prey or possibly differences in direct human influences (e.g., human-inflicted mortality, agricultural practices). Species that were more often common or more abundant in Canada than in the United States were the coyote, black-billed magpie, and American crow. Species that more often were common or more abundant in the United States than in Canada were the red fox, raccoon, mink, ferruginous hawk, and great horned owl. However, the species composition of predators and the abundance of individual predator species in individual study areas varied within and among parts of the prairie pothole region.

Implications for Duck Production

Although the effect of individual predator species on duck production in the prairie pothole region is largely undetermined, some investigators (Johnson et al. 1987; Klett et al. 1988) identified a trend of increasing nest success by ducks from east to west, probably from differences in the composition and abundance of predator species. However, only Johnson et al. (1989) attempted to relate nest success by ducks to abundance of predators. They found that rates of predation on duck nests early in the nesting season increased with the abundance indices of red foxes, badgers, and American crows and late in the season, with the abundance indices of red foxes and striped skunks. The red fox emerged as the principal predator. Other investigators (Duebbert and Lokemoen 1976; Higgins 1977; Sargeant et al. 1984; Klett et al. 1988) also identified the red fox as a major predator of ducks and duck eggs.

Because of differences in their behavior, food habits, and abundance, individual predator species affect duck production differently. Some species prey almost exclusively on eggs, others prey almost exclusively on adults and ducklings, and a few prey on all three. Moreover, different predator species affect ducks differently, depending on factors such as date of nesting by ducks and location of nests. For example, red foxes prey much more extensively on hens that nest in uplands than on hens that nest in wetlands (Sargeant et al. 1984), but minks do the reverse (Eberhardt and Sargeant 1977).

Among the predators we surveyed that prey on adult ducks, three species of mammals (coyote, red fox, mink), one mammal group (weasels), and four species of birds (northern harrier, Swainson's hawk, red-tailed hawk, great horned owl) were known or thought (weasels) to be common or numerous in one or more study areas (Tables 4 and 5) and thus sufficiently abundant to reduce survival of nesting female ducks. The number common or numerous of these species averaged 3.0 (SD = 1.26) per individual study area and always included the red fox, coyote, or both.

Predation on adult ducks was evidenced by partially consumed carcasses found each year in all study areas (A. B. Sargeant and R. J. Greenwood, unpublished data). No data on mortality of ducks were collected in the Central Flyway study areas. Remains of 573 adult ducks were found in the stabilized regulations study areas and remains of 224 adult ducks in the small unit management study areas and adjoining lands. The remains represented an undetermined but probably small portion of the depredated adult ducks. Sargeant et al. (1984) estimated that red foxes took over 800,000 adult ducks, mostly female dabblers, annually from the prairie pothole region during spring and early summer 1969–73. Twenty percent of the dead adult ducks we recovered were from red fox dens (above ground and in den entrances only). Ducks recovered in this manner during a single visit to one den of a red fox family represented on average 4.5% of the ducks taken by the family (Sargeant et al. 1984).

The abundance of red foxes has a profound effect on the survival of adult ducks in the prairie pothole region and should be monitored. However, other predators, especially coyotes and certain raptors, probably also prey extensively on adult ducks. Of 87 dead adult ducks found in study areas in Alberta, 83% were from study areas (Gayford, Hay Lakes, Holden) that had little to no evidence of minks, red foxes, and weasels; 67% were from one area (Hay Lakes) where coyotes (Appendix Tables 5 and 8) and red-tailed hawks (Appendix Table 15) were especially numerous.

In the prairie pothole region, annual duck production is most affected by destruction of nests (Cowardin and Johnson 1979; Klett et al. 1988).

Mayfield-corrected estimates of duck nest success (Johnson 1979) in the five principal species of dabbling ducks (mallard, gadwall [*Anas strepera*], blue-winged teal [*A. discors*], northern shoveler [*A. clypeata*], northern pintail [*A. acuta*]) ranged from 7 to 31% in Central Flyway study area-years and from 3 to 29% in stabilized regulations study area-years (Johnson et al. 1987; R. J. Greenwood, unpublished data). Comparable estimates were not available on ducks in the small unit management study areas, but other data for that part of the region show similarly low nest success (Klett et al. 1988). More than 85% of the destroyed nests were attributed to predation (Greenwood et al. 1987; Johnson et al. 1987; Klett et al. 1988).

All predator species we surveyed except raptors prey extensively on duck eggs, although predation by minks is primarily in wetlands and predation by gulls is primarily on islands (Sargeant and Arnold 1984; A. B. Sargeant, unpublished data). The number of common or numerous egg-eating species (excludes large gulls and weasels, which were not rated) averaged 4.6 (SD = 0.90) per study area (calculated from data in Tables 4 and 5). Only two study areas (Gayford, Courtenay) had less than four (three) common or numerous egg-eating species, and one of those (Gayford) was adjacent to a large nesting colony of ring-billed gulls and California gulls. Because of their great abundance, the gulls had potential for extensive predation on duck eggs in that study area. Thus, duck nests in all but one study area were at risk of predation by at least four predator species.

The average numbers of common or numerous egg-eating predator species per study area did not differ among provinces and states (4.0 in Alberta [SD = 0.82], 4.0 in Minnesota [SD = 0.00], 4.3 in South Dakota [SD = 0.58], 4.3 in North Dakota [SD = 0.87], 4.5 in Montana [SD = 0.71], 5.1 in Saskatchewan [SD = 0.88], and 6.0 in Manitoba [SD = 0.00]— calculated from data in Tables 4 and 5). However, species composition of common or numerous egg-eating predators differed among study areas in various parts of the prairie pothole region and reflected a gradual replacement of mammals by birds from southeast to northwest across the region. For example, all common and numerous egg-eating species in the United States were mammals, whereas birds comprised nearly half of such species in Alberta (Tables 4 and 5). The portion of the region with the greatest number of common or numerous egg-eating species was southwestern Manitoba and southeastern Saskatchewan where as many as seven such species were in individual study areas (Tables 4 and 5). Coyotes and red foxes were common or numerous in most study areas there, but often their presence in study areas was strongly segregated.

Among egg-eating predators, the striped skunk, American crow, and red fox probably have greatest effect on nest success of ducks in uplands, whereas the raccoon probably has greatest effect on nest success of ducks that nest over water. At least two of these predators were common or numerous in all study areas except one (Gayford). Although the red fox was largely absent from study areas in Alberta, it was replaced by high populations of coyotes (Figs. 5 and 7). Raccoons were common or numerous in all study areas in the eastern half of the prairie pothole region but were uncommon or less numerous in nearly all other study areas (Fig. 8). Unlike red foxes (A. B. Sargeant, unpublished data), coyotes are prone to entering water (Young and Jackson 1951; Hanson and Eberhardt 1971). In shallow wetlands in some study areas where coyotes were particularly abundant, they may have been major predators of clutches in over-water nests. The harm of avian egg-eating predators on clutches in over-water nests is largely undetermined. Sullivan and Dinsmore (1990), who studied artificial duck nests, suggested that clutches in over-water nests are less vulnerable than clutches in upland nests to predation by American crows. With the diverse community of egg-eating predators in all of our study areas, we concluded that duck eggs in nests throughout the prairie pothole region are at high risk of predation but that localized differences in predation rates should be expected.

The magnitude of predation on ducklings and the principal predator species of ducklings in the prairie pothole region are unclear. However, the principal predator species and species-groups affecting duckling survival probably should include all species that prey on adult ducks as well as the American crow, ferruginous hawk, and large gulls. Also, all predators of duck eggs probably prey on newly hatched ducklings discovered in nest bowls.

Considerably more data than are currently available are required to clarify interactions be-

tween predator populations and duck production in the prairie pothole region. However, because predation is a major factor of duck production throughout the region, the composition and abundance of predators will probably emerge as a major cause of variability in duck production. For this reason, we urge investigators of waterfowl recruitment to assess the composition of predator populations and abundance of predator species in their study areas. Such assessments should be as important as gathering information on habitat condition and composition. The information need not be detailed to be useful, and descriptive narratives with quantification of observations may suffice. The absence of a predator species can be as important as its presence. Where possible, however, we recommend use of systematic monitoring that permits comparison of findings with those of other studies. Our surveys were not labor-intensive and provided baseline data that can be used to gauge future changes in composition, abundance, and distribution of predators in the prairie pothole region.

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Appendix. Tables of supplementary data gathered in the prairie pothole region

Appendix Table 1. *Predator surveys in study areas in the prairie pothole region, 1983–88.*[a]

		Predator surveys and method of survey					
Area[b]	Years	Striped skunk (live-trapping)	Franklin's ground squirrel (livetrapping)	Carnivore tracks (counts)	Predator sightings (counts)	Corvids (road transect counts)	Avian predators (nest counts)
Canada							
Alberta							
Gayford	1985	x[c]	x	x	x	x	x
Hay Lakes*	1983–84	x	x	x	x	x	x
Holden*	1983	x	x	x	x	x	x
Penhold*	1984–85	x	x	x	x	x	x
Manitoba							
Cartwright	1983	x	x	x	x	x	x
Moore Park*	1983–84	x	x	x	x	x	x
Saskatchewan							
Ceylon	1983–84	x	x	x	x	x	x
Craik	1984–85	x	x	x	x	x	x
Denzil	1984–85	x	x	x	x	x	x
Earl Grey*	1985	x	x	x	x	x	x
Goodwater	1983	x	x	x	x	x	x
Hanley*	1983–85	x	x	x	x	x	x
Inchkeith*	1984–85	x	x	x	x	x	x
Leask*	1984–85	x	x	x	x	x	x[d]
Shamrock	1983–85	x	x	x	x	x	x
Yorkton*	1985	x	x	x	x	x	x
United States							
Minnesota							
Hawley*	1987–88			x	x		x
Hitterdal*	1988			x	x		x
Lake Park*	1987–88			x	x		x
Montana							
Plentywood	1983		x	x[e,f]	x	x	
Morgan	1983		x	x[e]	x	x	
North Dakota							
Courtenay	1988			x	x		x
Eldridge	1987–88			x	x		x
Fredonia	1987–88			x	x		x
Jud	1987–88			x	x		x
Kulm	1988			x	x		x
Litchville	1987–88			x	x		x
Plaza	1983		x	x[f]	x	x	
Sharon	1983		x	x[f]	x	x	
Streeter	1983		x	x[f]	x	x	

Appendix Table 1. *Continued.*

Area[b]	Years	Predator surveys and method of survey					
		Striped skunk (live-trapping)	Franklin's ground squirrel (livetrapping)	Carnivore tracks (counts)	Predator sightings (counts)	Corvids (road transect counts)	Avian predators (nest counts)
South Dakota							
Hosmer	1983		x	x[f]	x	x	
Madison	1983		x	x[f]	x	x	
Parkston	1983		x	x[f]	x	x	

[a] Searches were incomplete during 1983.
[b] Study areas denoted with an asterisk (*) are in the aspen parkland, all others are in the prairie.
[c] An (x) denotes that the particular survey was conducted annually during all indicated years.
[d] Searches limited to 21 quarter sections during 1984; included were searches in all quarter sections in the eastern 7.2 km of the study area.
[e] Only one search was conducted.
[f] Track search was limited to 19 quarter sections in the western 9.6 km of the study area.

Appendix Table 2. *Legal descriptions of reference points in study areas in the prairie pothole region where predator populations were assessed during 1 or more years, 1983–88.*[a]

Area[b]	Longitude of principal meridian	Township	Range	Section	Location in section
Canada					
Alberta					
Gayford	114° 00′00″	27N	26W	5	SW corner
Hay Lakes*	100° 00′00″	49N	21W	4	SW corner
Holden*	100° 00′00″	49N	14W	6	SW corner
Penhold*	114° 00′00″	37N	2W	4	SW corner
Manitoba					
Cartwright	98° 27′40″	1N	17W	21	SW corner of SE quarter
Moore Park*	98° 27′40″	13N	19W	9	SW corner of SE quarter
Saskatchewan					
Ceylon	102° 00′00″	5N	21W	27	SW corner
Craik	106° 00′00″	24N	2W	15	SW corner
Denzil	106° 00′00″	38N	25W	2	SW corner
Earl Grey*	102° 00′00″	23N	20W	4	SW corner
Goodwater	102° 00′00″	5N	14W	30	SW corner
Hanley*	106° 00′00″	31N	3W	16	SW corner
Inchkeith*	102° 00′00″	13N	5W	18	SW corner
Leask*	106° 00′00″	47N	5W	4	SW corner
Shamrock	106° 00′00″	15N	6W	4	SW corner
Yorkton*	102° 00′00″	26N	9W	14	SW corner
United States					
Minnesota					
Hawley*	91° 30′7″	139N	44W	15	center
Hitterdal*	91° 30′7″	141N	44W	36	center
Lake Park*	91° 30′7″	140N	42W	19	center
Montana					
Morgan	111° 30′7″	37N	30E	4	SW corner of NW quarter
Plentywood	111° 30′7″	37N	56E	2	SW corner of SW quarter
North Dakota					
Courtenay	91° 30′7″	139N	44W	15	center
Eldridge	91° 30′7″	139N	65W	25	center
Fredonia	91° 30′7″	132N	68W	4	center south edge
Jud	91° 30′7″	135N	66W	35	center
Kulm	91° 30′7″	131N	66W	1	center
Litchville	91° 30′7″	138N	59W	34	center
Plaza	91° 30′7″	153N	87W	32	SW corner
Sharon	91° 30′7″	148N	58W	13	SW corner
Streeter	91° 30′7″	137N	69W	19	SW corner
South Dakota					
Hosmer	91° 30′7″	124N	71W	6	SW corner
Madison	91° 30′7″	107N	53W	27	SW corner
Parkston	91° 30′7″	101N	64W	35	SW corner

[a] See Fig. 3 for location of reference points in study areas.
[b] Study areas denoted with an asterisk(*) are in the aspen parkland, all others are in the prairie.

Appendix Table 3. *Numbers of adult predators removed annually during April–June from tracts of federal land managed for waterfowl production in the center of each of three small unit management study areas in the prairie pothole region, 1987–88.*

Area	Year	Size of tract (ha)	Species							
			Red fox	Raccoon	Striped skunk	Badger	Mink	Ermine	Long-tailed weasel	Franklin's ground squirrel
Minnesota										
Lake Park	1987	63	0	11	22	0	2	1	0	0
	1988	128	2	6	22	1	1	0	0	0
North Dakota										
Eldridge	1987	65	2	0	7	0	0	0	0	12
	1988	65	0	1	6	0	0	0	0	4
Fredonia	1987	303	0	5	20	1	0	0	8	13
	1988	303	1	4	26	2	0	0	2	7

Appendix Table 4. *Average percentage of quarter sections in which black-billed magpies and American crows were seen or heard during repeated counts along road transect on the 16-km center-road of stabilized regulations and Central Flyway study areas in the prairie pothole region during May to early July, 1983–85.*

Area[a]	Year	Number of counts	Percentage of quarter sections: Black-billed magpie	Percentage of quarter sections: American crow
Canada				
Alberta				
Gayford	1985	12	1.9	14.8
Hay Lakes*	1983	14	3.2	9.5
	1984	12	4.6	18.3
Holden*	1983	13	3.5	42.5
Penhold*	1984	12	11.9	21.5
	1985	12	3.1	12.9
Manitoba				
Cartwright	1983	15	2.7	10.0
Moore Park*	1983	13	1.5	14.4
	1984	12	1.9	7.9
Saskatchewan				
Ceylon	1983	12	0.0	2.7
	1984	12	0.0	5.6
Craik	1984	12	1.3	21.7
	1985	12	0.8	22.5
Denzil	1984	12	0.4	16.5
	1985	12	0.6	17.9
Earl Grey*	1985	12	1.9	18.3
Goodwater	1983	14	0.2	5.4
Hanley*	1983	15	5.3	45.2
	1984	12	4.8	40.4
	1985	12	2.1	32.1
Inchkeith*	1984	9	3.3	9.7
	1985	11	3.2	12.5
Leask*	1984	12	0.0	12.1
	1985	12	0.2	9.6
Shamrock	1983	14	0.0	6.3
	1984	12	0.0	7.7
	1985	12	0.0	13.5
Yorkton*	1985	12	1.9	14.4
United States				
Montana				
Morgan	1983	7	0.0	0.0
Plentywood	1983	9	0.0	1.1
North Dakota				
Plaza	1983	9	0.0	0.0
Sharon	1983	9	0.0	0.6
Streeter	1983	9	0.0	0.3
South Dakota				
Hosmer	1983	6	0.0	0.8
Madison	1983	9	0.0	2.2
Parkston	1983	9	0.0	1.7

[a] Study areas denoted with an asterisk (*) are in the aspen parkland, all others are in the prairie. No counts were made in the small unit management study areas.

Appendix Table 5. *Annual percentage of searched quarter sections in study areas in the prairie pothole region where tracks of specified carnivore species were found one or more times during two searches for tracks in April–June 1983–88.*

Area[a]	Year	Searched quarter sections (N)	Percent of quarter sections with tracks						
			Coyote	Gray wolf	Red fox	Raccoon	Striped skunk	Badger	Mink
Canada									
Alberta									
Gayford	1985	40	88	0	0	0	13	30	0
Hay Lakes*	1983	40	100	0	7	0	67	0	0
	1984	40	100	0	0	0	60	0	0
Holden*	1983	40	100	0	7	2	65	5	0
Penhold*	1984	40	75	0	27	0	50	15	0
	1985	38	84	0	26	0	39	0	0
Manitoba									
Cartwright	1983	40	45	0	65	27	38	15	0
Moore Park*	1983	40	22	10	60	70	57	17	5
	1984	39	72	0	44	18	38	10	0
Saskatchewan									
Ceylon	1983	40	60	0	47	65	52	35	0
	1984	39	64	0	56	51	54	28	5
Craik	1984	39	54	0	64	26	87	5	3
	1985	40	57	0	92	35	90	0	0
Denzil	1984	40	47	0	88	0	85	7	0
	1985	40	22	0	97	0	82	2	0
Earl Grey*	1985	40	95	0	38	17	45	5	0
Goodwater	1983	40	38	0	45	32	52	32	0
Hanley*	1983	40	100	0	20	7	75	30	0
	1984	39	92	0	21	8	82	18	0
	1985	40	100	0	30	10	70	10	0
Inchkeith*	1984	39	95	0	69	49	62	41	0
	1985	40	82	0	77	63	63	40	0
Leask*	1984	40	97	0	27	2	80	38	0
	1985	40	97	0	38	5	63	20	0
Shamrock	1983	39	82	0	31	15	49	38	0
	1984	40	88	0	30	22	57	35	0
	1985	40	65	0	35	13	20	27	0
Yorkton*	1985	40	100	0	5	80	63	5	0
United States									
Minnesota									
Hawley*	1987	36	0	0	89	86	42	3	50
	1988	31	0	0	100	68	58	0	61
Hitterdal*	1988	33	0	0	97	88	61	0	55
Lake Park*	1987	35	0	0	97	94	51	6	43
	1988	33	0	0	100	94	64	3	67
Montana									
Morgan[b]	1983	36	14(31)	0	17(35)	0(9)	69(87)	53(71)	—[c]
Plentywood[b]	1983	19	42(59)	0	58(74)	16(30)	95(100)	74(97)	—[c]
North Dakota									
Courtenay	1988	36	3	0	100	75	53	14	22
Eldridge	1987	36	42	0	86	69	44	22	0
	1988	33	27	0	88	52	36	21	3
Fredonia	1987	34	47	0	35	56	47	15	9
	1988	36	47	0	53	72	64	31	39
Jud	1987	36	67	0	81	86	39	31	28
	1988	32	75	0	53	72	47	31	13

Appendix Table 5. *Continued.*

Area[a]	Year	Searched quarter sections (N)	Percent of quarter sections with tracks: Coyote	Gray wolf	Red fox	Raccoon	Striped skunk	Badger	Mink
Kulm	1988	36	47	0	81	75	31	28	28
Litchville	1987	36	0	0	97	75	81	6	17
	1988	35	0	0	100	66	49	23	34
Plaza[b]	1983	39	5(22)	0	69(85)	55(80)	36(62)	18(29)	—[c]
Sharon[b]	1983	40	0(17)	0	88(100)	40(61)	70(87)	17(28)	—[c]
Streeter[b]	1983	40	47(64)	0	57(74)	65(94)	42(67)	82(100)	—[c]
South Dakota									
Hosmer[b]	1983	40	7(25)	0	42(60)	35(55)	44(67)	17(28)	—[c]
Madison[b]	1983	40	2(20)	0	45(62)	67(98)	5(39)	22(34)	—[c]
Parkston[b]	1983	34	9(26)	0	59(75)	79(100)	47(70)	50(68)	—[c]

[a] Study areas denoted with an asterisk (*) are in the aspen parkland, all others are in the prairie.

[b] A single track search was conducted during May or late June. Values in parenthesis are estimated percentages of searched quarter sections in which tracks would have been found had two searches been conducted and are based on correlations of data from twice-searched study areas.

[c] No data available.

Appendix Table 6. *Comparisons of the percentage of study areas in the prairie pothole region of Canada and the United States with studied predator species rated* common *or more abundant, 1983–88. Weasels and large gulls were excluded because data were insufficient to rate the abundance of these species.*

	Study areas in Canada			Study areas in United States[a]				
Species	(N)	No. ≥ common	% ≥ common	(N)	No. ≥ common	% ≥ common	$\chi^{2b,c}$	*P*
Carnivores								
Coyote	16	16	100	17	8	47	11.65	0.001
Gray wolf	16	0	0	17	0	0	0.01	0.977
Red fox	16	11	69	17	17	100	6.26	0.012
Raccoon	16	7	44	17	16	94	9.90	0.002
Striped skunk	16	15	94	17	17	100	1.10	0.295
Badger	16	6	37	17	10	59	1.50	0.221
Mink	16	0	0	9	5	56	11.11	0.001
Rodents								
Franklin's ground squirrel	16	3	19	17	0	0	3.51	0.061
Corvids								
Black-billed magpie	16	6	37	17	0	0	7.79	0.005
American crow	16	15	94	17	0	0	29.22	<0.001
Raven	16	0	0	17	0	0	0.01	0.977
Raptors								
Northern harrier	16	7	44	9	1	11	2.82	0.093
Swainson's hawk	15[d]	7	47	9	4	44	0.01	0.916
Red-tailed hawk	16	8	50	9	2	22	1.85	0.174
Ferruginous hawk	16	0	0	9	2	22	3.87	0.049
Great horned owl	16	6	38	9	8	89	6.17	0.013

[a] Excludes minks and raptors in eight Central Flyway study areas because data were insufficient to determine whether abundance was common or greater.

[b] Chi-square value with 1 df.

[c] We added 0.5 to all cells to accommodate zero counts.

[d] Excludes the Holden study area because data were insufficient to determine whether species was common or more abundant.

Appendix Table 7. *Comparisons of percentage of study areas in the prairie and in the aspen parkland habitat zones of the prairie pothole region having abundance of individual predator species rated common or more abundant, 1983–88. Weasels and large gulls were excluded because data were insufficient to rate abundance.*

	Study areas in prairie[a]			Study areas in aspen parkland				
Species	(N)	No. ≥ common	% ≥ common	(N)	No. ≥ common	% ≥ common	$\chi^{2b,c}$	*P*
Carnivores								
Coyote	21	15	72	12	9	75	0.05	0.825
Gray wolf	21	0	0	12	0	0	0.07	0.787
Red fox	21	20	95	12	8	67	4.85	0.028
Raccoon	21	17	81	12	6	50	3.46	0.063
Striped skunk	21	20	95	12	12	100	0.59	0.443
Badger	21	14	67	12	2	17	7.64	0.006
Mink	13	2	15	12	3	25	0.36	0.548
Rodents								
Franklin's ground squirrel	21	0	0	12	3	25	5.78	0.016
Corvids								
Black-billed magpie	21	1	5	12	5	42	6.99	0.008
American crow	21	6	29	12	9	75	6.64	0.010
Raven	21	0	0	12	0	0	0.07	0.787
Raptors								
Northern harrier	13	4	31	12	4	33	0.02	0.891
Swainson's hawk	13	9	69	11[d]	2	18	6.25	0.012
Red-tailed hawk	13	1	8	12	10	83	14.49	<0.001
Ferruginous hawk	13	2	15	12	0	0	2.01	0.157
Great horned owl	13	8	62	12	6	50	0.34	0.561

[a] Excludes minks and raptors in eight Central Flyway study areas because data were insufficient to determine whether abundance was common or greater.
[b] Chi-square value with 1 df.
[c] We added 0.5 to all cells to accommodate zero counts.
[d] Excludes the Holden study area because data were insufficient to determine whether species was common or more abundant.

Appendix Table 8. *Number of occupied rearing dens of coyotes and red foxes in study areas in the prairie pothole region and estimated number of represented families (study areas in which no dens were found were excluded), 1983–88. Dens over 1.6 km apart were assumed to represent different families.*[a]

		Coyote		Red fox	
Area[b]	Year	Dens	Families	Dens	Families
Canada					
Alberta					
Gayford	1985	1	1	0	0
Hay Lakes*	1983	2	2	0	0
	1984	5	4	0	0
Penhold*	1985	0	0	1	1
Manitoba					
Cartwright	1983	0	0	1	1
Moore Park*	1983	0	0	1	1
Saskatchewan					
Ceylon	1984	0	0	4	2
Craik	1984	0	0	4	4
	1985	0	0	3	2
Denzil	1984	0	0	1	1
	1985	0	0	3	1
Goodwater	1983	0	0	3	2
Hanley*	1984	0	0	1	1
Inchkeith*	1984	0	0	4	3
	1985	0	0	3	1
Leask*	1984	0	0	1	1
	1985	0	0	1	1
	1984	1	1	0	0
Yorkton*	1985	3	2	0	0
United States					
Minnesota					
Hawley*	1987[c]	0	0	3	3
	1988[c]	0	0	5	3
Hitterdal*	1988[c]	0	0	5	3
Lake Park*	1987[c]	0	0	3	2
	1988[c]	0	0	2	2
Montana					
Plentywood	1983	0	0	1	1
North Dakota					
Courtenay	1988[c]	0	0	2	1
Eldridge	1987[c]	0	0	2	2
	1988[c]	0	0	1	1
Fredonia	1987[c]	1	1	2	2
	1988[c]	2	1	7	3
Jud	1987[c]	1	1	0	0
	1988[c]	0	0	2	1
Kulm	1988[c]	0	0	2	1
Litchville	1987[c]	0	0	5	3
	1988[c]	0	0	9	4
Plaza	1983	0	0	1	1
Sharon	1983	0	0	1	1
Streeter	1983	0	0	1	1
South Dakota					
Hosmer	1983	0	0	1	1

[a] Based on Sargeant et al. (1975).
[b] Study areas denoted with an asterisk (*) are in aspen parkland, all others are in prairie.
[c] Includes dens found during aerial searches.

Appendix Table 9. *Capture rates of striped skunks in study areas in the prairie pothole region of Canada during nighttime livetrapping in early May, 1983–85.*

Area[a]	Year	Trap-nights	Captures	Capture rate (×10)
Alberta				
Gayford	1985	200	1	0.05
Hay Lakes*	1983	198	5	0.25
	1984	200	8	0.40
Holden*	1983	200	5	0.25
Penhold*	1984	195	5	0.26
	1985	180	4	0.22
Manitoba				
Cartwright	1983	200	3	0.15
Moore Park*	1983	197	8	0.41
	1984	199	9	0.45
Saskatchewan				
Ceylon	1983	159	9	0.57
	1984	200	16	0.80
Craik	1984	194	21	1.08
	1985	200	16	0.80
Denzil	1984	190	13	0.68
	1985	200	4	0.20
Earl Grey*	1985	200	8	0.40
Goodwater	1983	200	9	0.45
Hanley*	1983	200	12	0.60
	1984	195	22	1.13
	1985	200	25	1.25
Inchkeith*	1984	199	5	0.25
	1985	200	9	0.45
Leask*	1984	194	7	0.36
	1985	200	4	0.20
Shamrock	1983	195	5	0.26
	1984	200	4	0.20
	1985	200	5	0.25
Yorkton*	1985	200	6	0.30

[a] Study areas denoted with an asterisk (*) are in the aspen parkland, all others are in the prairie.

Appendix Table 10. *Average number of places per hour (observation rate) where one or more individuals of each mammalian predator species were seen in study areas in the prairie pothole region, 1983–88.*[a]

Area[b]	Year	Observer hours	Observation rate ($\times 10^3$) Coyote	Red fox	Raccoon	Striped skunk	Badger	Mink	Weasels[c]	Franklin's ground squirrel
Canada										
Alberta										
Gayford	1985	822	71	0	0	0	15	0	4	0
Hay Lakes*	1983	888	12	0	0	0	0	0	6	6
	1984	1,085	29	0	0	2	1	0	0	0
Holden*	1983	830	14	1	0	4	0	0	2	6
Penhold*	1984	762	17	0	0	4	0	0	3	0
	1985	769	16	1	0	5	1	0	0	0
Manitoba										
Cartwright	1983	586	3	7	2	0	0	0	0	10
Moore Park*	1983	774	1	4	1	3	4	0	3	61
	1984	920	1	0	2	3	0	0	0	16
Saskatchewan										
Ceylon	1983	935	1	3	2	10	9	0	2	0
	1984	608	10	13	2	12	2	0	0	2
Craik	1984	606	2	23	0	7	0	0	0	3
	1985	636	0	6	2	30	0	0	0	3
Denzil	1984	870	0	7	0	1	0	0	1	0
	1985	1,084	1	8	0	6	2	0	1	0
Earl Grey*	1985	868	2	0	0	2	0	0	0	1
Goodwater	1983	825	7	24	1	11	0	0	0	5
Hanley*	1983	867	5	6	0	4	1	0	0	9
	1984	852	9	1	0	11	0	0	0	6
	1985	1,215	8	2	0	21	1	0	0	9
Inchkeith*	1984	624	14	32	0	2	0	0	2	10
	1985	813	0	10	0	3	0	0	0	12
Leask*	1984	1,167	1	2	0	1	0	0	0	1
	1985	1,403	3	2	0	1	1	0	1	0
Shamrock	1983	950	2	0	0	2	0	0	2	0
	1984	561	2	0	0	11	0	0	4	0
	1985	547	11	29	0	0	4	0	0	2
Yorkton*	1985	1,087	5	0	6	7	0	0	2	6
United States										
Minnesota										
Hawley*	1987	859	0	9	2	6	0	2	0	0
	1988	718	0	19	1	8	1	1	1	1
Hitterdal*	1988	1,251	0	10	2	1	0	4	1	6
Lake Park*	1987	875	0	13	0	3	0	3	0	5
	1988	731	0	8	5	0	1	4	0	0
Montana										
Morgan	1983	290	0	24	0	0	3	0	0	0
Plentywood	1983	435	7	7	0	28	0	0	0	0
North Dakota										
Courtenay	1988	469	0	21	0	13	0	0	0	0
Eldridge	1987	932	1	28	0	0	0	0	0	2
	1988	286	0	45	0	7	0	0	0	3
Fredonia	1987	1,456	7	5	2	3	1	1	5	8
	1988	776	4	15	0	6	0	0	4	3
Jud	1987	798	5	9	3	0	0	0	1	8
	1988	365	14	14	5	8	0	3	0	0
Kulm	1988	1,668	2	20	4	2	1	2	0	2

Appendix Table 10. *Continued.*

Area[b]	Year	Observer hours	Observation rate (×10^3) Coyote	Red fox	Raccoon	Striped skunk	Badger	Mink	Weasels[c]	Franklin's ground squirrel
Litchville	1987	910	0	41	2	3	0	1	0	3
	1988	355	0	110	3	0	0	3	0	0
Plaza	1983	453	0	16	0	7	0	0	7	0
Sharon	1983	514	0	82	0	2	0	0	2	12
Streeter	1983	416	5	24	2	12	0	0	0	2
South Dakota										
Hosmer	1983	431	0	53	0	9	0	0	5	0
Madison	1983	471	0	0	0	30	0	0	6	0
Parkston	1983	458	0	9	2	31	7	0	2	2

[a] A place is defined as 0.4 ha.
[b] Study areas denoted with an asterisk (*) are in the aspen parkland, all others are in the prairie.
[c] Predominantly long-tailed weasels but includes ermines.

Appendix Table 11. *Capture rates of Franklin's ground squirrels in early July during 24-h livetrapping in stabilized regulations and Central Flyway study areas in the prairie pothole region and percentages of 2.59 km^2 units of each study area in which this predator was captured, 1983–85.*

Area[a]	Year	Trap-days	Captures	Capture rate(×10)	Units with captures (%)
Canada					
Alberta					
Gayford	1985	200	0	0.00	0
Hay Lakes*	1983	200	2	0.10	20
	1984	200	0	0.00	0
Holden*	1983	200	2	0.10	10
Penhold*	1984	200	0	0.00	0
	1985	200	0	0.00	0
Manitoba					
Cartwright	1983	200	0	0.00	0
Moore Park*	1983	200	9	0.45	60
	1984	200	23	1.15	80
Saskatchewan					
Ceylon	1983	200	1	0.05	10
	1984	200	0	0.00	0
Craik	1984	200	0	0.00	0
	1985	200	0	0.00	0
Denzil	1984	200	0	0.00	0
	1985	200	0	0.00	0
Earl Grey*	1985	200	33	1.65	30
Goodwater	1983	200	10	0.50	40
Hanley*	1983	200	42	2.10	90
	1984	200	45	2.25	90
	1985	200	25	1.25	70
Inchkeith*	1984	200	19	0.95	50
	1985	200	14	0.70	40
Leask*	1984	200	5	0.25	30
	1985	200	2	0.10	10
Shamrock	1983	200	0	0.00	0
	1984	200	1	0.05	10
	1985	200	0	0.00	0
Yorkton*	1985	200	5	0.25	30
United States					
Montana					
Morgan	1983	0	—	—	—
Plentywood	1983	196	0	0.00	0
North Dakota					
Plaza	1983	200	0	0.00	0
Sharon	1983	200	1	0.05	10
Streeter	1983	199	4	0.20	30
South Dakota					
Hosmer	1983	199	0	0.00	0
Madison	1983	200	0	0.00	0
Parkston	1983	200	0	0.00	0

[a] Study areas denoted with an asterisk (*) are in the aspen parkland, all others are in the prairie. No livetrapping of this type was conducted in the small unit management study areas.

Appendix Table 12. *Number of occupied incidentally found nests of black-billed magpies and densities of occupied nests of American crows found in all wooded habitat during complete searches of study areas in the prairie pothole region, 1983–88.*

Area[a]	Year	Black-billed magpie: Found nests	American crow: Searched quarter sections	American crow: Found nests	American crow: Nest/10 km^{2b}
Canada					
Alberta					
Gayford	1985	0	40	15	5.8
Hay Lakes*	1983	0	—	3[c]	(2.6)
	1984	1	40	11	4.3
Holden*	1983	1	—	8[c]	(16.6)
Penhold*	1984	4	40	19	7.3
	1985	4	35	5	2.2
Manitoba					
Cartwright	1983	1	—	1[c]	(2.8)
Moore Park*	1983	0	—	1[c]	(4.7)
	1984	5	40	6	2.3
Saskatchewan					
Ceylon	1983	0	—	4[c]	(0)
	1984	0	39	2	0.8
Craik	1984	5	38	15	6.1
	1985	0	40	13	5.0
Denzil	1984	5	40	11	4.3
	1985	3	40	18	7.0
Earl Grey*	1985	2	40	9	3.5
Goodwater	1983	0	—	2[c]	(0.9)
Hanley*	1983	5	—	11[c]	(17.7)
	1984	9	39	40	15.8
	1985	0	40	49	18.9
Inchkeith*	1984	6	40	13	5.0
	1985	8	38	9	3.7
Leask*	1984	0	21	6	4.4
	1985	2	40	18	6.9
Shamrock	1983	0	—	1[c]	(0)
	1984	0	40	10	3.9
	1985	0	40	9	3.5
Yorkton*	1985	2	40	10	3.9
United States					
Minnesota					
Hawley*	1987	0	35	0[d]	0
	1988	0	33	2	0.9
Hitterdal*	1988	0	33	1	0.5
Lake Park*	1987	0	30	0[e]	0
	1988	0	33	1	0.5
Montana					
Morgan	1983	0	—	—	(0)
Plentywood	1983	0	—	—[f]	(0)
North Dakota					
Courtenay	1988	0	36	0	0
Eldridge	1987	0	36	0	0
	1988	0	35	0	0
Fredonia	1987	0	36	0	0
	1988	0	36	0	0
Jud	1987	0	36	1	0.4

Appendix Table 12. *Continued.*

Area[a]	Year	Black-billed magpie	American crow		
		Found nests	Searched quarter sections	Found nests	Nest/10 km^{2}[b]
	1988	0	32	0	0
Kulm	1988	0	36	0	0
Litchville	1987	0	36	0	0
	1988	0	36	0	0
Plaza	1983	0	—	—	(0)
Sharon	1983	0	—	—	(0)
Streeter	1983	0	—	—	(0)
South Dakota					
Hosmer	1983	0	—	—	(0)
Madison	1983	0	—	—	(0)
Parkston	1983	0	—	—	(0)

[a] Study areas denoted with an asterisk (*) are in the aspen parkland, all others are in the prairie.

[b] Estimates (in parentheses) were made with data from road-transect counts (Appendix Table 4) and based on the correlation ($r = 0.84$) between numbers of located nests and average percentage of quarter sections in which American crows were detected in study areas in Canada during 1984 and 1985.

[c] Searches for American crow nests were incomplete.

[d] One occupied nest was thought to have been present.

[e] Three occupied nests were thought to have been present.

[f] One occupied American crow nest was found incidentally in this study area; no occupied American crow nests were found in any other Central Flyway study area.

Appendix Table 13. *Average number of places per hour (observation rate) where one or more individuals of each avian predator species and species-group were seen in study areas in the prairie pothole region, 1983–88.*[a]

Area[b]	Year	Observer hours	Observation rate (×10³) American crow[c]	Black-billed magpie[c]	Large hawks[c,d]	Great horned owl
Canada						
Alberta						
Gayford	1985	822	1,814	1,849	1,805	6
Hay Lakes*	1983	888	1,805	1,773	1,938	26
	1984	1,085	1,795	1,527	1,686	20
Holden*	1983	830	2,938	1,717	1,761	15
Penhold*	1984	762	1,785	2,001	1,880	17
	1985	769	2,046	2,211	1,835	22
Manitoba						
Cartwright	1983	586	2,135	1,694	1,629	7
Moore Park*	1983	774	1,937	1,523	1,677	39
	1984	920	2,066	1,129	2,050	47
Saskatchewan						
Ceylon	1983	935	1,560	17	1,693	16
	1984	608	1,670	0	1,920	7
Craik	1984	606	2,012	1,650	1,702	13
	1985	636	2,087	1,061	1,829	17
Denzil	1984	870	1,768	1,179	1,793	16
	1985	1,084	1,717	772	1,835	6
Earl Grey*	1985	868	2,148	1,313	1,840	16
Goodwater	1983	825	1,760	282	1,908	14
Hanley*	1983	867	2,283	1,816	2,058	16
	1984	852	2,021	1,475	1,712	14
	1985	1,215	2,195	1,417	1,629	17
Inchkeith*	1984	624	2,158	2,077	2,116	24
	1985	813	1,727	1,667	1,747	14
Leask*	1984	1,167	1,755	558	1,767	7
	1985	1,403	1,681	486	1,642	2
Shamrock	1983	950	1,693	155	1,720	10
	1984	561	2,065	193	1,835	36
	1985	547	2,062	113	2,131	15
Yorkton*	1985	1,087	1,650	1,012	1,677	9
United States						
Minnesota						
Hawley*	1987	859	54	0	146	21
	1988	718	164	0	181	18
Hitterdal*	1988	1,251	155	1[e]	129	14
Lake Park*	1987	875	174	0	101	31
	1988	731	349	0	231	21
Montana						
Morgan	1983	290	107	0	1,852	0
Plentywood	1983	435	1,338	36	1,766	0
North Dakota						
Courtenay	1988	469	2	0	207	19
Eldridge	1987	932	2	0	156	48
	1988	286	10	0	462	63
Fredonia	1987	1,456	2	0	504	9
	1988	776	3	0	601	15
Jud	1987	798	19	0	358	20
	1988	365	22	0	438	60
Kulm	1988	1,668	47	0	482	11

Appendix Table 13. *Continued.*

Area[b]	Year	Observer hours	Observation rate (×10³) American crow[c]	Black-billed magpie[c]	Large hawks[c,d]	Great horned owl
Litchville	1987	910	2	0	193	13
	1988	355	8	0	535	31
Plaza	1983	453	241	0	1,249	11
Sharon	1983	514	317	0	1,176	2
Streeter	1983	416	75	0	1,697	10
South Dakota						
Hosmer	1983	431	1,187	36	2,504	7
Madison	1983	471	1,648	0	1,647	19
Parkston	1983	458	508	0	1,475	0

[a] A place is defined as 0.4 ha.

[b] Study areas denoted with an asterisk (*) are in the aspen parkland, all others are in the prairie.

[c] Data collected in 1983–85 cannot be compared with data collected in 1987–88 because of differences in recording procedures (see *Recording Sightings of Predators* section).

[d] Nearly all were northern harriers, Swainson's hawks, red-tailed hawks, and ferruginous hawks.

[e] Represented the sighting of a single black-billed magpie by one person.

Appendix Table 14. *Species composition (%) of large hawks in study areas in the prairie pothole region; based on daily tabulations of sightings of large hawks, 1983–88.*

Area[a]	Year	Sightings (*N*)	Percentage of total observations: Northern harrier	Swainson's hawk	Red-tailed hawk	Ferruginous hawk
Canada						
Alberta						
Gayford	1985	324	11	64	25	0
Hay Lakes*	1983	133	45	8	47	0
	1984	257	8	18	74	0
Holden*	1983	230	39	10	50	0
Penhold*	1984	204	22	13	62	3
	1985	104	10	36	54	0
Manitoba						
Cartwright	1983	63	41	30	29	0
Moore Park*	1983	94	46	26	29	0
	1984	409	27	8	65	0
Saskatchewan						
Ceylon	1983	236	53	46	0	1
	1984	204	39	59	0	2
Craik	1984	94	73	21	5	0
	1985	148	41	45	13	1
Denzil	1984	257	32	48	19	2
	1985	464	33	36	29	2
Earl Grey*	1985	145	28	50	19	3
Goodwater	1983	307	61	37	0	3
Hanley*	1983	128	51	25	24	0
	1984	207	65	8	26	1
	1985	262	52	27	20	1
Inchkeith*	1984	269	16	32	52	0
	1985	202	14	39	47	0
Leask*	1984	271	41	10	48	0
	1985	299	28	3	69	0
Shamrock	1983	305	47	47	0	6
	1984	250	36	61	0	3
	1985	165	44	53	0	2
Yorkton*	1985	183	18	2	80	0
United States						
Minnesota						
Hawley*	1987	118	6	0	91	0
	1988	138	18	0	80	0
Hitterdal*	1988	234	55	0	41	0
Lake Park*	1987	89	38	0	62	0
	1988	188	51	0	44	0
Montana						
Morgan	1983	227	41	42	0	17
Plentywood	1983	125	60	40	0	0
North Dakota						
Courtenay	1988	130	60	25	15	0
Eldridge	1987	105	22	63	13	0
	1988	175	49	32	15	2
Fredonia	1987	718	69	19	<1	11
	1988	566	69	18	2	11
Jud	1987	228	51	41	4	4
	1988	206	50	36	9	5
Kulm	1988	1,074	52	35	8	5
Litchville	1987	140	12	74	14	0
	1988	205	30	44	24	0

Appendix Table 14. *Continued.*

Area[a]	Year	Sightings (N)	Percentage of total observations: Northern harrier	Swainson's hawk	Red-tailed hawk	Ferruginous hawk
Plaza	1983	69	76	17	1	6
Sharon	1983	71	31	56	13	0
Streeter	1983	133	41	29	0	30
South Dakota						
Hosmer	1983	99	30	26	8	35
Madison	1983	30	17	70	13	0
Parkston	1983	44	2	71	27	0

[a] Study areas denoted with an asterisk (*) are in the aspen parkland, all others are in the prairie.

Appendix Table 15. *Number and density (nests/km^2) of occupied raptor nests in study areas in the prairie pothole region, 1983–88.*

Area[a]	Year	Searched quarter sections	Northern harrier N	Northern harrier Nest/km^2	Swainson's hawk N	Swainson's hawk Nest/km^2	Red-tailed hawk N	Red-tailed hawk Nest/km^2	Ferruginous hawk N	Ferruginous hawk Nest/km^2	Great horned owl N	Great horned owl Nest/km^2
Canada												
Alberta												
Gayford	1985	40	(1)[b]	(0.04)	4	0.15	3	0.12	0		0	
Hay lakes*	1983	—	(4)	(0.15)	(0)		(11)	(0.42)	0		(2)	(0.08)
	1984	40	(0)		3	0.12	19	0.73	(0)		1	0.04
Holden*	1983	—	(4)	(0.15)	(0)		(4)	(0.15)	0		(2)	(0.08)
Penhold*	1984	40	(1)	(0.04)	1	0.04	7	0.27	(0)		0	
	1985	35	(0)		0		2	0.09	0		0	
Manitoba												
Cartwright	1983	—	(1)	(0.04)	(0)		(1)	(0.04)	(0)		0	
Moore Park*	1983	—	(6)	(0.23)	(0)		(4)	(0.15)	(0)		(0)	
	1984	40	(1)	(0.04)	1	0.04	6	0.23	0		1	0.04
Saskatchewan												
Ceylon	1983	—	(8)	(0.31)	4	0.15	0		(0)		0	
	1984	39	(4)	(0.16)	6	0.24	0		0		0	
Craik	1984	38	(2)	(0.08)	1	0.04	0		0		1	0.04
	1985	40	(0)		1	0.04	0		0		1	0.04
Denzil	1984	40	(0)		3	0.12	0		0		1	0.04
	1985	40	(0)		4	0.15	2	0.08	0		0	
Earl Grey*	1985	40	(1)	(0.04)	2	0.08	2	0.08	0		0	
Goodwater	1983	—	(14)	(0.54)	4	0.15	0		0		1	0.04
Hanley*	1983	—	(2)	(0.08)	(1)	(0.04)	(0)		(0)		(0)	
	1984	39	(1)	(0.04)	0		0		0		1	0.04
	1985	40	(2)	(0.08)	1	0.04	0		0		1	0.04
Inchkeith*	1984	40	(0)		3	0.12	2	0.08	0		0	
	1985	38	(0)		1	0.04	3	0.12	0		1	0.04
Leask*	1984	21	(3)	(0.22)	0		2	0.15	0		0	
	1985	40	(3)	(0.12)	0		6	0.23	0		0	
Shamrock	1983	—	(2)	(0.08)	2	0.08	0		0		1	0.04
	1984	40	(8)	(0.31)	2	0.08	0		0		1	0.04
	1985	40	(5)	(0.19)	4	0.15	0		0		0	
Yorkton*	1985	40	(1)	(0.04)	0		4	0.15	0		1	0.04
United States[c]												
Minnesota												
Hawley*	1987	35	(0)		0		5	0.22	0		1	0.04
	1988	33	(0)		0		4	0.19	0		4	0.19
Hitterdal*	1988	33	(1)	(0.05)	0		3	0.14	0		2	0.09
Lake Park*	1987	30	(0)		0		2	0.10	0		0	
	1988	33	(0)		0		0		0		1	0.05

Appendix Table 15. *Continued.*

Area[a]	Year	Searched quarter sections	Species: Northern harrier N	Northern harrier Nest/km^2	Swainson's hawk N	Swainson's hawk Nest/km^2	Red-tailed hawk N	Red-tailed hawk Nest/km^2	Ferruginous hawk N	Ferruginous hawk Nest/km^2	Great horned owl N	Great horned owl Nest/km^2
North Dakota												
Courtenay	1988	36	(1)	(0.04)	2	0.09	1	0.04	0		1	0.04
Eldridge	1987	36	(0)		3	0.13	0		0		2	0.09
	1988	35	(0)		0		0		0		0	
Fredonia	1987	36	(15)	(0.67)	3	0.13	0		3	0.13	1	0.04
	1988	36	(3)	(0.13)	3	0.13	0		2	0.09	1	0.04
Jud	1987	36	(0)		4	0.17	0		0		1	0.04
	1988	32	(0)		3	0.14	0		0		2	0.10
Kulm	1988	36	(1)	(0.04)	1	0.04	0		2	0.09	1	0.04
Litchville	1987	36	(0)		3	0.13	0		0		1	0.04
	1988	36	(0)		2	0.09	1	0.04	0		1	0.04

[a] Study areas denoted with an asterisk (*) are in the aspen parkland; all other study areas are in the prairie.

[b] Numbers in parentheses represent incomplete counts of nests because some quarter sections were not completely searched (1983 only) or nest site selection prevented obtaining complete counts (northern harrier).

[c] Excludes the eight Central Flyway study areas where data on raptor nests were limited to incidental observations. Species and numbers of nests of each species in those study areas were: Morgan (Swainson's hawk [four], ferruginous hawk [one]); Plentywood (northern harrier [two]); Streeter (northern harrier [one], Swainson's hawk [one], ferruginous hawk [one]); Plaza (northern harrier [two], Swainson's hawk [one], great horned owl [one]); and Parkston (red-tailed hawk [one]).

A list of current *Resource Publications* follows.

174. Obsolete English Names of North American Birds and Their Modern Equivalents, by Richard C. Banks. 1988. 37 pp.
175. Procedures for the Analysis of Band-recovery Data and User Instructions for Program MULT, by Michael J. Conroy, James E. Hines, and Byron K. Williams. 1989. 61 pp.
176. Sago Pondweed (*Potamogeton pectinatus* L.): A Literature Review, by Harold A. Kantrud. 1990. 90 pp.
177. Field Manual for the Investigation of Fish Kills, by Fred P. Meyer and Lee A. Barclay, editors. 1990. 120 pp.
178. Section 404 and Alterations in the Platte River Basin of Colorado, by Douglas N. Gladwin, Mary E. Jennings, James E. Roelle, and Duane A. Asherin. 1992. 19 pp.
179. Hydrology of the Middle Rio Grande From Velarde to Elephant Butte Reservoir, New Mexico, by Thomas F. Bullard and Stephen G. Wells. 1992. 51 pp.
180. Waterfowl Production on the Woodworth Station in South-central North Dakota, 1965–1981, by Kenneth F. Higgins, Leo M. Kirsch, Albert T. Klett, and Harvey W. Miller. 1992. 79 pp.
181. Trends and Management of Wolf–Livestock Conflicts in Minnesota, by Steven H. Fritts, William J. Paul, L. David Mech, and David P. Scott. 1992. 27 pp.
182. Selection of Prey by Walleyes in the Ohio Waters of the Central Basin of Lake Erie, 1985–1987, by David R. Wolfert and Michael T. Burr. 1992. 14 pp.
183. Effects of the Lampricide 3-Trifluoromethyl- 4-Nitrophenol on the Pink Heelsplitter, by Terry D. Bills, Jeffrey J. Rach, Leif L. Marking, and George E. Howe. 1992. 7 pp.
184. Methods for Detoxifying the Lampricide 3-Trifluoromethyl-4-Nitrophenol in a Stream, by Philip A. Gilderhus, Terry D. Bills, and David A. Johnson. 1992. 5 pp.
185. Group Decision-making Techniques for Natural Resource Management Applications, by Beth A. K. Coughlan and Carl L. Armour. 1992. 55 pp.
186. DUCKDATA: A Bibliographic Data Base for North American Waterfowl (Anatidae) and Their Wetland Habitats, by Kenneth J. Reinecke and Don Delnicki. 1992. 7 pp.
187. Dusky Canada Goose: An Annotated Bibliography, by Bruce H. Campbell and John E. Cornely. 1992. 30 pp.
188. Human Disturbances of Waterfowl: An Annotated Bibliography, by Robert B. Dahlgren and Carl E. Korschgen. 1992. 62 pp.
189. Opportunities to Protect Instream Flows and Wetland Uses of Water in Nevada, by James L. Bingham and George A. Gould. 1992. 33 pp.
190. Assessment of Habitat of Wildlife Communities on the Snake River, Jackson, Wyoming, by Richard L. Schroeder and Arthur W. Allen. 1992. 21 pp.
191. Evaluating Temperature Regimes for Protection of Smallmouth Bass, by Carl L. Armour. 1993. 26 pp.
192. Sensitivity of Juvenile Striped Bass to Chemicals Used in Aquaculture, by Terry D. Bills, Leif L. Marking, and George E. Howe. 1993. 11 pp.
193. Introduction of Foxes to Alaskan Islands — History, Effect on Avifauna, and Eradication, by Edgar P. Bailey. 1993. 52 pp.

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